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CHAPTER 10

The Bottlenosed Dolphin in Biomedical Research

SAM H. RIDGWAY

I. Introduction

The Cetacea (whales) are a mammalian order whose ancestors, about 60 million years ago, left the dry land for the water. In their evolution to completely aquatic life these mammals have made many interesting physiological and anatomical adaptations (Howell, 1930). Their bodies have become elongated and streamlined. Their forelimbs have become paddlelike flippers, and the rear appendages have disappeared except for a vestigial pelvis, to which attaches the crura of the penis in the male. Occasionally whales are found with vestigial femurs and more rarely primitive rear limbs. The tail has become the primary organ of locomotion through flattened, elongated projections of tough, fibrous tissue called flukes. The external ear has all but disappeared. Only a vestigial ear canal remains. Subdermally, adjacent to the tiny ear canal, there is a vestige of the pinna. The physiology of these animals has also adapted to function in the aquatic environment. Respiratory functions, thermoregulatory mechanisms, circulation, and renal physiology have undergone significant changes that are reflected in some anatomical variations.

The Cetacea are divided into two suborders. The Mysticeti, or baleen whales, and the Odontoceti, or toothed whales. The baleen whales, of which there are about a dozen species, are so called because of the baleen, or whalebone, by which they strain their food from the seawater. The baleen consists of rows of horny plates which depend from the roof of their mouth. The ventral edges of the baleen plates are frayed, forming hairlike projections which make an efficient strainer. The small life which constitutes most of the baleen whale's diet is collectively called krill. The largest of all living animals, the blue whale, *Baleonoptera musculus,* is a baleen whale. Larger members of this species may grow to 100 feet in length, and weights of well over 100 tons have been recorded. Unfortunately, this species is now almost extinct because of its exploitation by the whaling industry.

The Odontoceti or toothed whales number about seventy species, and as the name suggests they have teeth. Rather than subsisting on krill, the Odontocetes consume chiefly fishes and squids. The toothed whales range in size from the harbor porpoise, *Phocaena phocaena*, which attains an average length of 4–5 feet to the sperm whale, *Physeter catodon*, which grows to 70 feet and weighs as many tons. The smaller members of the toothed whales consist of about forty-five species that are called dolphins or porpoises.

Of all the Cetaceans the Atlantic bottlenose porpoise, *Tursiops truncatus*, must be considered to be the best known. The first attempts to maintain these animals in captivity were made at the New York Aquarium. Townsend (1918) describes the establishment of a small group there, but unfortunately they died out in a relatively short time. Marineland of the Atlantic, St. Augustine, Florida, established the first permanent colony of captive porpoises in 1938. Today there are about twenty-five oceanariums, zoos, amusement parks, and research laboratories in the United States that maintain porpoises. They are also kept in Japan, Canada, Australia, New Zealand, South Africa, Denmark, France, Great Britain, and perhaps other countries.

Porpoises and Dolphins

Probably the question most frequently asked by laymen about Cetaceans is, "What is the difference between a porpoise and a dolphin?" F. G. Wood, Jr., who was formerly Curator of Marineland of the Atlantic and is currently Head of the Navy Marine Bioscience Facility, answers it this way:

> "Seafarers and coast dwellers of English-speaking countries generally call all of these little whales porpoises. Even most authorities in the United States think that porpoise is a perfectly good word for any small Cetacean. Also, as a name for the mammal, it helps avoid confusion with the fish called the dolphin.
>
> "Dolphin, however, is used in the literary world and by most European scientists. The word dolphin has had a long history. It has come down to us from the Greek word for dolphin, *delphis*. The old spelling is preserved in the scientific name of the family to which most of these animals belong, the Delphinidae. The dolphins the Greeks knew were slender, long-snouted animals which played a prominent part in ancient Greek literature and art.
>
> "The word porpoise has had a long history, too. In England a few hundred years ago it was spelled porpess. This word came from the Old French *porpeis* which, in turn, can be traced to the Latin *porcus piscis* meaning pork fish or fish hog.
>
> "The original *porcus piscis* was evidently a small (five to six foot) whale with a blunt head and spade-shaped teeth. Today it is known as the common or harbor porpoise. It is the most abundant small cetacean in the Atlantic coastal waters of Europe.

"Fishermen considered it a fish hog because they thought it devoured many fish that rightfully belonged in their nets. They called it *porcus piscis,* and in the course of many hundreds of years the words ran together to become porpoise. To fishermen all of the same cetaceans were fish hogs or "herring-hogs"—all were porpoises.

"This has now become the common usage. But some people still prefer to call only the harbor porpoise and its close relatives by this name. All others they consider to be dolphins. It is, as you see, largely a matter of personal preference."

II. Anatomy

A. External Anatomy

1. *Body Parts and Terms*

Tursiops is a fairly large, stout-bodied porpoise reaching 10–12 feet in length; 8 feet is a more usual maximum length for the species. Maximum

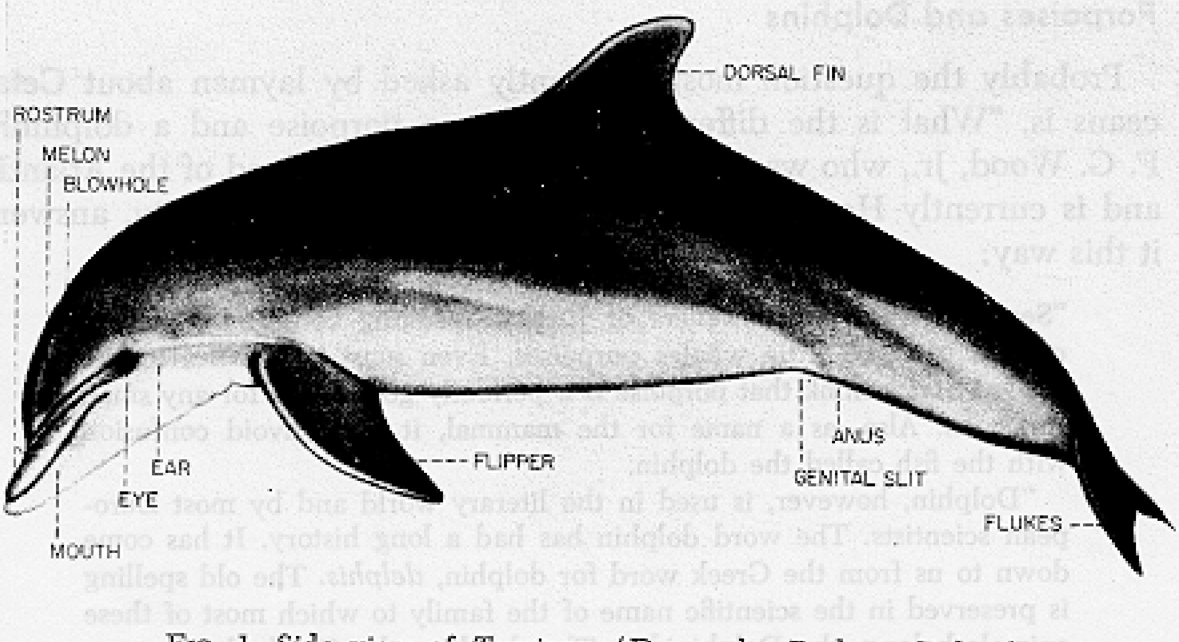


FIG. 1. Side view of *Tursiops.* (Drawn by Barbara Stolen.)

body weight of mature individuals is usually between 250 and 500 pounds. Individual specimens as large as 800 pounds are occasionally encountered. The common name "bottlenose" is derived from the prominent beak (Fig. 1) formed by the elongated upper and lower jaws. The lower jaw is usually about 0.5–1.5 cm longer than upper.

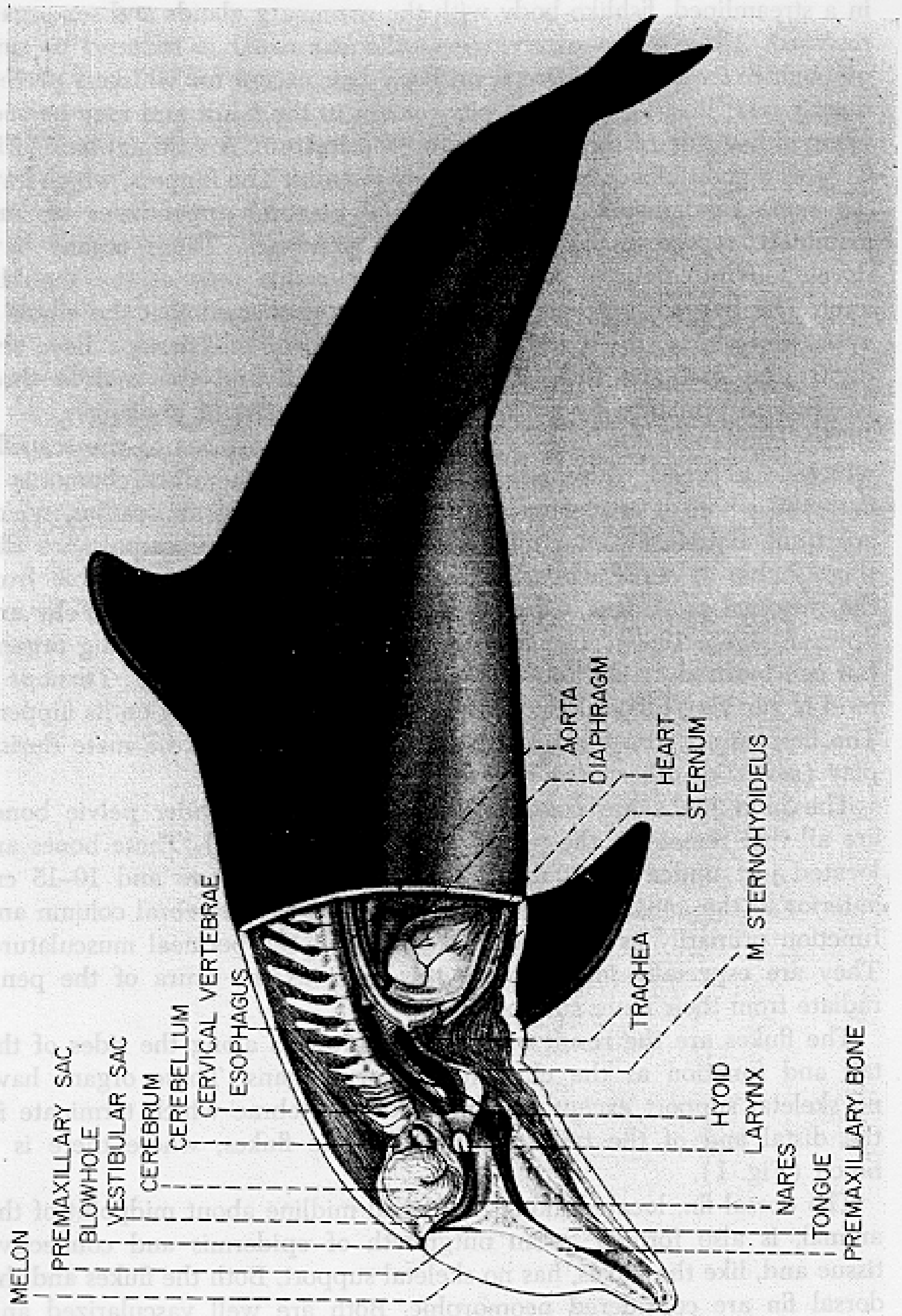
The bluntly tapered head and trunk appear to merge, as there is no externally visible neck because of shortening and fusing of the cervical vertebrae (Fig. 2). Adaptation to the marine environment has resulted in a streamlined, fishlike body with the mammary glands and sex organs recessed. There is no external ear—the ear canal is reduced to tiny, pinpoint-like opening. There is no body hair except for whiskers present during fetal life. The whisker pits remain in the adult and may be seen along either side of the upper jaw on the rostrum. A vestigial hair (Fig. 3) with a good blood and nerve supply remains. The flippers, which have the same fundamental structure as the pectoral appendages of land mammals, represent the only paired appendages. These organs have developed into flat, fin-shaped paddles movable only at the shoulder joint. The humerus, radius, and ulna are so shortened that the elbow is approximately at the body trunk. The flippers in *Tursiops* have five digits; the first and fifth are highly reduced, and the middle three lengthened primarily by an increase in the number of phalanges.

The humerus has a large globular head and attaches to the scapula, which is a broad, flattened, fan-shaped bone. The distal humerus is flattened where it articulates with the proximal ulna and radius, which are quite flattened and parallel to one another. The carpals are distinguishable as such, while the metacarpals are indistinguishable from the proximal phalanges, especially of the three longer digits (Felts and Spurrell, 1965, 1966). The flippers are used mainly as steering organs, but can be used as paddles to back up and as water brakes. *Tursiops* is fond of carrying bits of kelp, seaweed, or a dead fish along on its flippers. The flippers are also used to partially grasp or to stroke a mate during play (sexual or otherwise).

The hind limbs are completely lacking; short, slender pelvic bones are all that remain of the pelvic girdle (Burne, 1952). These bones are located just under the blubber about 10–15 cm above and 10–15 cm anterior to the anus. They are not attached to the vertebral column and function primarily as areas for attachment of the perineal musculature. They are especially important in the male, as the crura of the penis radiate from their inner surface.

The flukes are the result of lateral outgrowths along the sides of the tail and function as the chief locomotory organs. These organs have no skeletal support except for the caudal vertebrae which terminate in the distal end of the tail stalk between the flukes, where there is a notch (Fig. 1).

The dorsal fin, located along the dorsal midline about midpoint of the animal, is also formed as an outgrowth of epidermis and connective tissue and, like the flukes, has no skeletal support. Both the flukes and the dorsal fin are considered neomorphic. Both are well vascularized and play an important role in temperature regulation.


MELON
PREMAXILLARY SAC
BLOWHOLE
VESTIBULAR SAC
CEREBRUM
CEREBELLUM
CERVICAL VERTEBRAE
ESOPHAGUS
AORTA
DIAPHRAGM
HEART
STERNUM
M. STERNOHYOIDEUS
TRACHEA
HYOID
LARYNX
NARES
TONGUE
PREMAXILLARY BONE

2. *Teeth and Age Determination*

The mouth is quite broad and deep; it is considered to be subterminal in that the lower jaw is normally about 0.5–1.5 cm longer than the upper. The teeth, which number one hundred or so, are uniform, peglike, one-

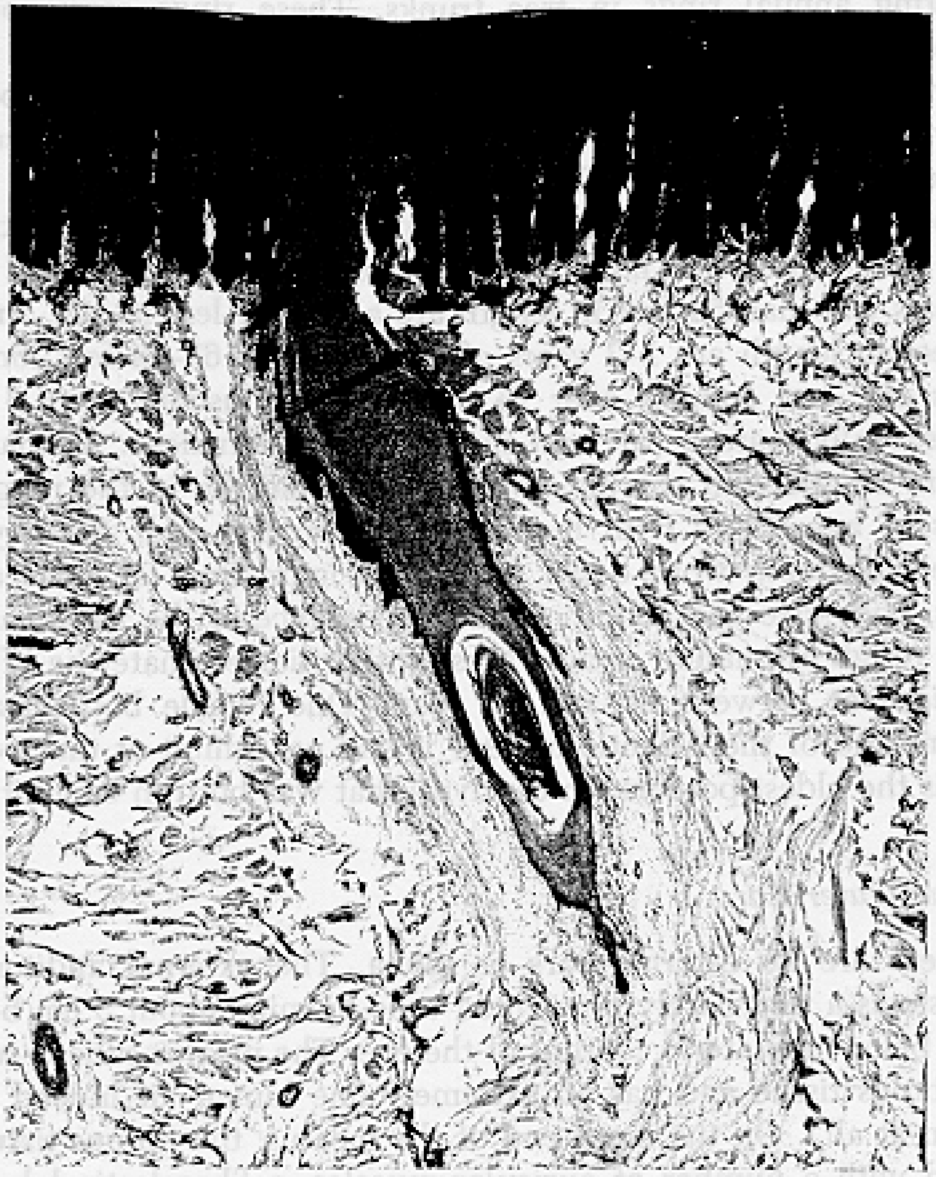


FIG. 3. Photomicrograph of skin section through a whisker pit on the upper rostrum. ×20.

root with a small central pulp cavity. All the teeth erupt in a fairly short period of time starting at about 6 weeks of age; they are conical in shape, curve slightly toward the end, and are round in cross section. Older animals will exhibit teeth worn on the end, and in some individuals

FIG. 2. Side view of head with certain internal anatomy exposed. The left lung has been removed. (Drawn by Barbara Stolen from dissection by Robert F. Green.)

of advanced age the teeth are worn right down to the gum. Only very rough estimates of age can be made from this criterion.

Ages of *Tursiops* and some other cetaceans (Nishiwaki and Yagi, 1954) and seals (Laws, 1953) have been estimated by counting the number of rings in cross sections of the roots of the teeth, much like counting annual rings in tree trunks. These rings correspond to the deposition of dentine on the inner surface of the pulp cavity in concentric layers. Sergeant (1959) reported that clear dentine was laid down during early spring at the time of mating, when nutrition is possibly suboptimal, and opaque dentine is laid down during the rest of the year.

Body size is another criterion that may be used in rough estimation of age. In general, but no doubt with considerable individual variation, animals less than 5½ feet in length are a year or less in age. Animals 5½–6½ feet in length are 1–3 years of age. Animals 6½–7½ feet long are 3–6 years old, and animals over 7½ feet long are usually over 6 years old and sexually mature (at least in the case of females). Animals over 7½ feet in length with sharply pointed teeth may be in the range of 5–10 years of age; those with teeth rounded on the end, 10–15 years, and those with teeth worn down toward the gum line, 20 years and older. Thus, body size and condition and appearance of the teeth can be used for a rough estimation of age. Most authorities estimate the life span for *Tursiops* at between 30 and 40 years. One female bottlenose born at Marineland of the Atlantic in 1947 is still on exhibit at that oceanarium and is the oldest porpoise in captivity that was born in captivity.

3. *The Outer Ear*

There are no external ears or pinna. The external auditory meatus persists as a tiny darkly pigmented tube opening about 5 cm behind and 2 cm below the lateral canthus of the eye. The meatus tube is surrounded by fibrous tissue and has an extremely fine lumen (if indeed there is a lumen at all). On the inner end of the meatus, the fibrous tissue is associated with a number of auricular muscles, a fibroelastic lobe, and the auricular cartilage, which appears to be homologous to the ear pinna of other mammals (Purves and Van Utrecht, 1963).

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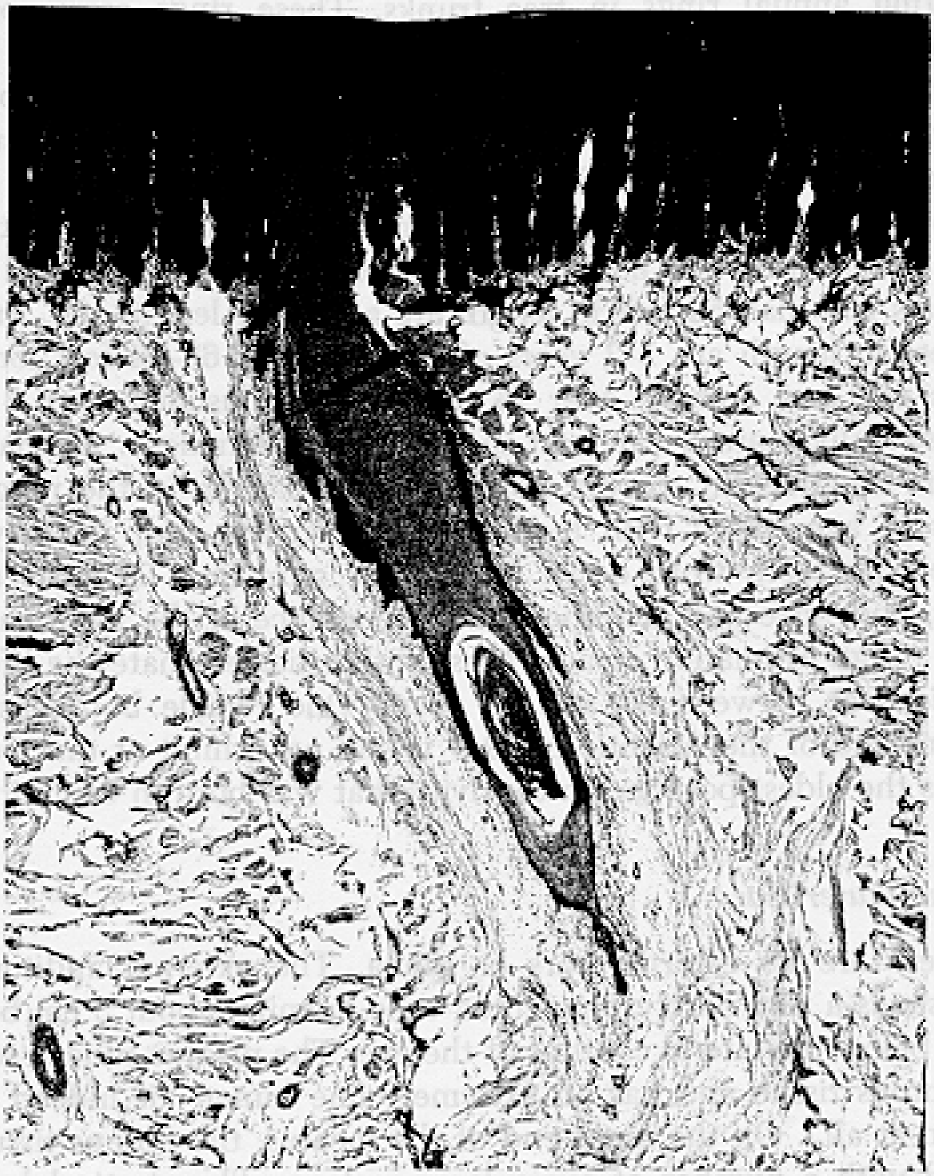

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The female has a somewhat longer single slit (sometimes, but improperly, called the cloacal orifice) which houses the vaginal orifice, the urethral orifice, and the anus in its posterior part (Fig. 4). In some

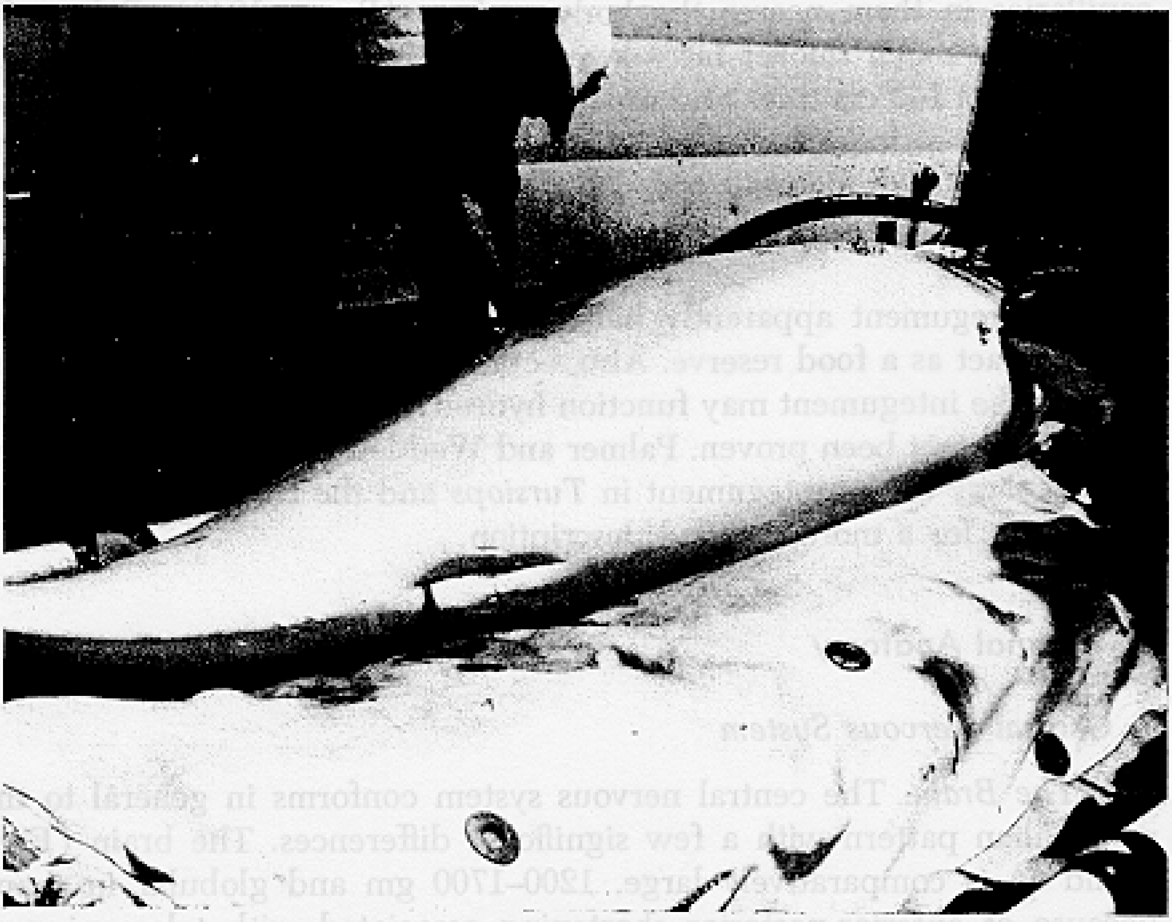

FIG. 4. View of underside of a female *Tursiops* showing external genitalia and anus. The mammary slits containing the recessed nipples are seen on either side of the genital slit. An intramuscular injection is being given.

individuals the anus appears as a separate external opening, as in the male. Slightly mid-lateral to this slit are two or more much smaller slits which house the nipples; these are recessed flush with the body surface except when lactating.

5. *Integument*

Tursiops is dark gray to black above with a lighter white to pink undersurface. The skin is smooth and hairless and has no sebaceous or sweat glands. The epidermis is about 1 mm thick and bounded below by a much thinner, tough connective tissue dermis.

These two layers are bound tightly together by many fingerlike dermal papillae oriented along longitudinal ridges and projecting into the epidermal layer, almost to the external surface (Fig. 3). These papillae not only form a tight connection between the two layers but place the capillaries in them nearer the body surface (Parry, 1949). Below the dermis is a much thicker fatty layer called the hypodermis or blubber. This layer is 1–2 cm thick and separated from the muscle fascia below by a thin layer of loose connective tissue. The hypodermis or blubber, the dermis, and the epidermis are grossly contiguous and together form a tough, fibrous integument that feels smooth, soft, and rubbery to the touch.

This integument apparently helps in streamlining, aids in insulation, and may act as a food reserve. Also, acting together with muscles underlying it, the integument may function hydrodynamically in reducing drag, but this has not been proven. Palmer and Weddell (1964) have examined the histology of the integument in *Tursiops* and the reader is referred to their work for a more detailed description.

B. Internal Anatomy

1. *Central Nervous System*

a. The Brain. The central nervous system conforms in general to the mammalian pattern with a few significant differences. The brain (Figs. 2 and 5) is comparatively large. 1200–1700 gm and globular in shape because of anterior-posterior shortening associated with telescoping of the skull (G. S. Miller, 1923). The cerebral hemispheres are large and highly convoluted (Langworthy, 1931, 1932). The fissures and sulci show marked opercularization of the deep cortical segments. The large temporal lobes form a prominent feature of the hemispheres when viewed ventrally.

On the ventral surface of the frontal lobe can be seen a smooth area just anterior to the optic chiasma containing the caudate nucleus. Thus, the caudate nucleus is exposed. This is not the case in other mammals. The thalamus is relatively large. The cerebral peduncles and large pons are rather short and wide. The prominent inferior accessory olive can be seen on the ventral surface of the medulla.

The cerebellum is also large and well differentiated. Particular attention has been called to the enlarged paraflocculus (associated with trunk and tail sensory perception); likewise the lobulus simplex and paramedian lobule are enlarged. The anterior hemispheres, ansiform lobule, and flocculonodular lobe are reduced, apparently because of less need for equilibration in water. The development of the cerebellum in general is thought to be due to the necessity for coordination of swimming movements.

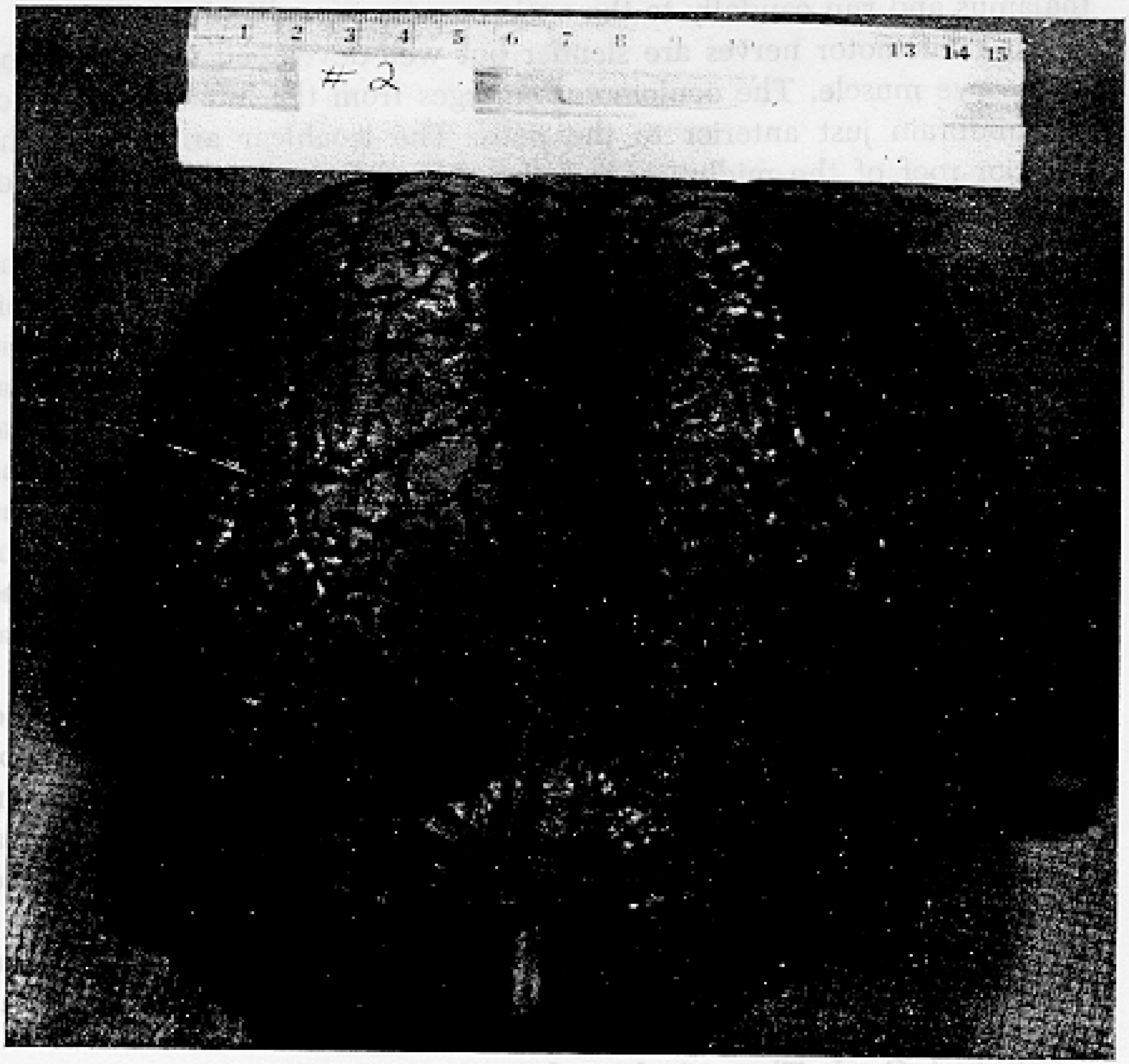

FIG. 5. Dorsal view of the brain of *Tursiops*.

The large and apparently well-developed brain of *Tursiops* has been the subject of much interest and speculation. The brain-to-body length, brain-to-body weight, and brain-to-spinal cord ratios are greater than those of any other animal except man (Ridgway *et al.*, 1966). Many factors must be considered in any attempts to evaluate the large brain. Among these are the echolocation capability, ecology, and possible level of intelligence.

b. Cranial Nerves. The olfactory nerves, tracts, and lobes are missing in Odontocetes. The nerves and tracts were possibly pinched off over millions of years of evolution by mechanical destructive forces at the cribriform plate (R. Kellogg, 1931).

The optic nerves, the most anterior of the cranial nerves, are well developed. According to Langworthy (1932), all the fibers decussate in the chiasma. The fibers circle around the posterior border of the thalamus and run caudally to the optic or superior colliculi.

The oculomotor nerves are slender but well-developed nerves leading to the eye muscle. The oculomotor emerges from the inferior surface of the midbrain just anterior to the pons. The trochlear arises from the anterior roof of the midbrain, and the abducens at the anterior end of the medulla.

The trigeminal is one of the two largest cranial nerves attached to the pons as a single solid trunk. The ophthalmic branch leads to the orbit and nasal regions, the maxillary branch to the upper jaw, and the mandibular branch to the skin and teeth of the lower jaw. The facial nerves exit from the lateral medulla and pass forward along the bulla, below the orbit, to the facial region, where the fibers innervate the blowhole muscles, the auricular muscles, etc. The auditory nerve is the largest of the cranial nerves, the cochlear division exceeding the vestibular in size. These divisions emerge from the lateral surface of the medulla just behind the facial root and pass laterally a centimeter or so to the ear.

The glossopharyngeal, vagus, and accessory nerves are closely related anatomically as well as functionally. They are concerned in regulation of vital processes associated with respiration, circulation, and digestion (Breathnach, 1960). Each arises from the ventrolateral medulla by a series of rootlets. Their fibers innervate such organs as the pharynx, the larynx, the stomach, the bronchi, and the lungs.

The hypoglossal nerve arises from the ventral medulla lateral to the olivary eminence. The fibers innervate the tongue and the gular musculature (Lawrence and Schevill, 1965).

c. Spinal Cord. The spinal cord terminates in an extensive cauda equina at the level of the third lumbar vertebra (Green, 1968). The relative external location of the cauda equina is ventral to the anterior portion of the dorsal fin. Its histology has not previously been investigated, but it is currently under study by Flanigan, who described the spinal cord of *Lagenorhynchus obliquidens* (1966).

2. *Respiratory System*

a. Blowhole and Nares. Cetaceans breathe through a modified nasal orifice called the blowhole. In Mysticetes the nostrils are paired at the surface, thus there is a paired blowhole. In Odontocetes including *Tursiops*, however, the organ appears at the surface of the forehead as a single transversely crescenteric opening with the concavity facing forward. A septum a few centimeters down the respiratory passage divides the nostril into two passages. The septum begins as membranously covered cartilage and continues as a bony divider. These passages unite again some 10–12 cm below the point where the bony septum begins.

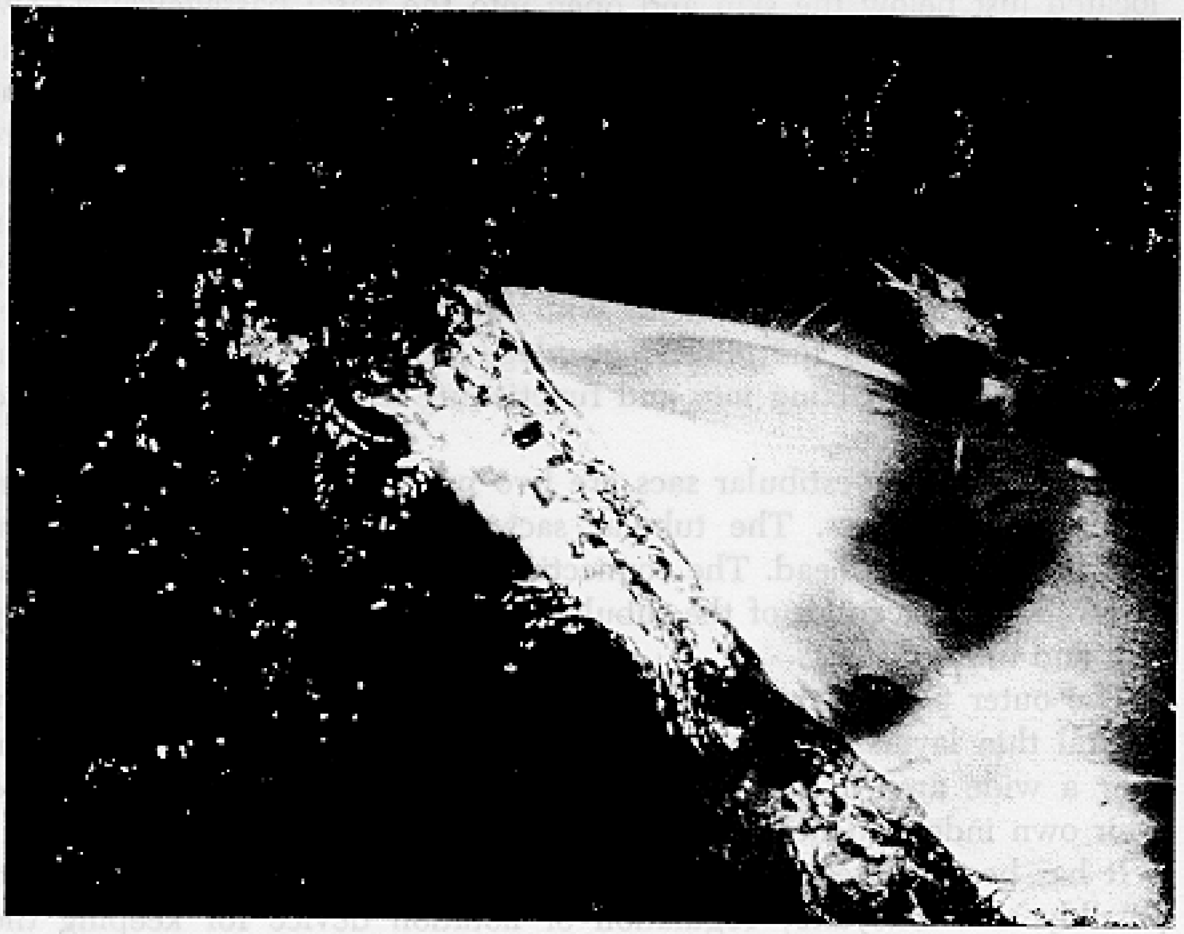

FIG. 6. View of blowhole as a porpoise breathes.

Closure of the blowhole is accomplished by a muscular nasal plug (Fig. 6). The migration of the nasal orifice from the end of the rostrum (the usual position in land mammals) to the highest point on the forehead provides a distinct advantage for a swimming mammal who must frequently rise to the surface to breathe. Thus with the functioning of sphincter-like muscles around the blowhole and the strong nasal plug, the animal can take a breath while swimming at full speed through the water. Lawrence and Schevill (1956) have demonstrated that *Tursiops* can take a breath (expiration and inspiration) in 0.3 second. Thus, with a tidal volume of 5–10 liters of air (Irving *et al.*, 1941), the flow rates through the air passages would range from approximately 30 liters to 70 liters per second during expiration and inspiration. The muscles that control the blowhole mechanism act primarily in contracting to open the orifice, thus the nasal plug and blowhole are in a closed position except when opened by muscular action (Huber, 1934). The vestibular and tubular sacs that relate directly to the nares also probably contribute to the closure of the passage and blowhole.

b. Air Sacs. An extensive system of membranes, sacs, and tubes are located just below the skin and open into the nasal passageway (Lawrence and Schevill, 1956). The vestibular sacs, located just below the skin in the superficial layers of blowhole musculature, open into the lateral nasal passage just below the lips of the blowhole. These sacs are directed posterolaterally, and together with the passage form a widened vestibular area. The largest of these sacs, the *premaxillary sacs,* lie on top of the premaxillary bone just anterior to the opening into the bony nares. Their lining is continuous with the lining of the nasal passages and the covering of the *plugs.* The *plugs* are formed of masses of connective tissue projecting into and functioning to occlude the upper end of the nasal passage.

Just below the vestibular sacs are two pairs of much smaller *tubular* and *connecting* sacs. The tubular sacs are U-shaped and lie almost horizontally in the head. The connecting sacs appear to be small lateral and ventral projections of the tubular sacs and connect the premaxillary sacs and tubular sacs.

The outer part of the nasal passage and the sacs are surrounded by several thin layers of blowhole musculature, most of which take origin over a wide area in the frontomaxillary region. The nasal plugs have their own independent musculature.

It has been suggested that the nasal air sacs act as a water trap and possibly as a buoyancy regulation or flotation device for keeping the blowhole above water when the animal is resting or sleeping (Purves, 1967). They may also function in sound production and in osmoregulation (Coulombe *et al.,* 1965) by reclaiming some of the water that might otherwise be lost through the breath.

c. Larynx. The larynx has become highly specialized to give a direct route between the internal nares and the lungs, allowing the *Tursiops* to breathe through the blowhole only. The larynx has developed into an elongated, tubular, spoutlike organ projecting 8–10 cm up from the floor of the nasopharynx with the upper end held in the internal nares by a muscular sphincter formed of palotopharyngeal musculature (Fig. 2).

This tubular larynx is called the "arytenoepiglottal" tube, as most modifications upon the basic mammalian plan are modifications in the epiglottal and arytenoid cartilages. These cartilages have become elongated to form the beaklike projection of the larynx. The anterior epiglottal cartilage has a posterior-dorsal grooved surface forming a trough into which the folded arytenoid cartilages fit. The thyroid and cricoid cartilages are present, but show little modification.

There is currently some controversy among scientists interested in

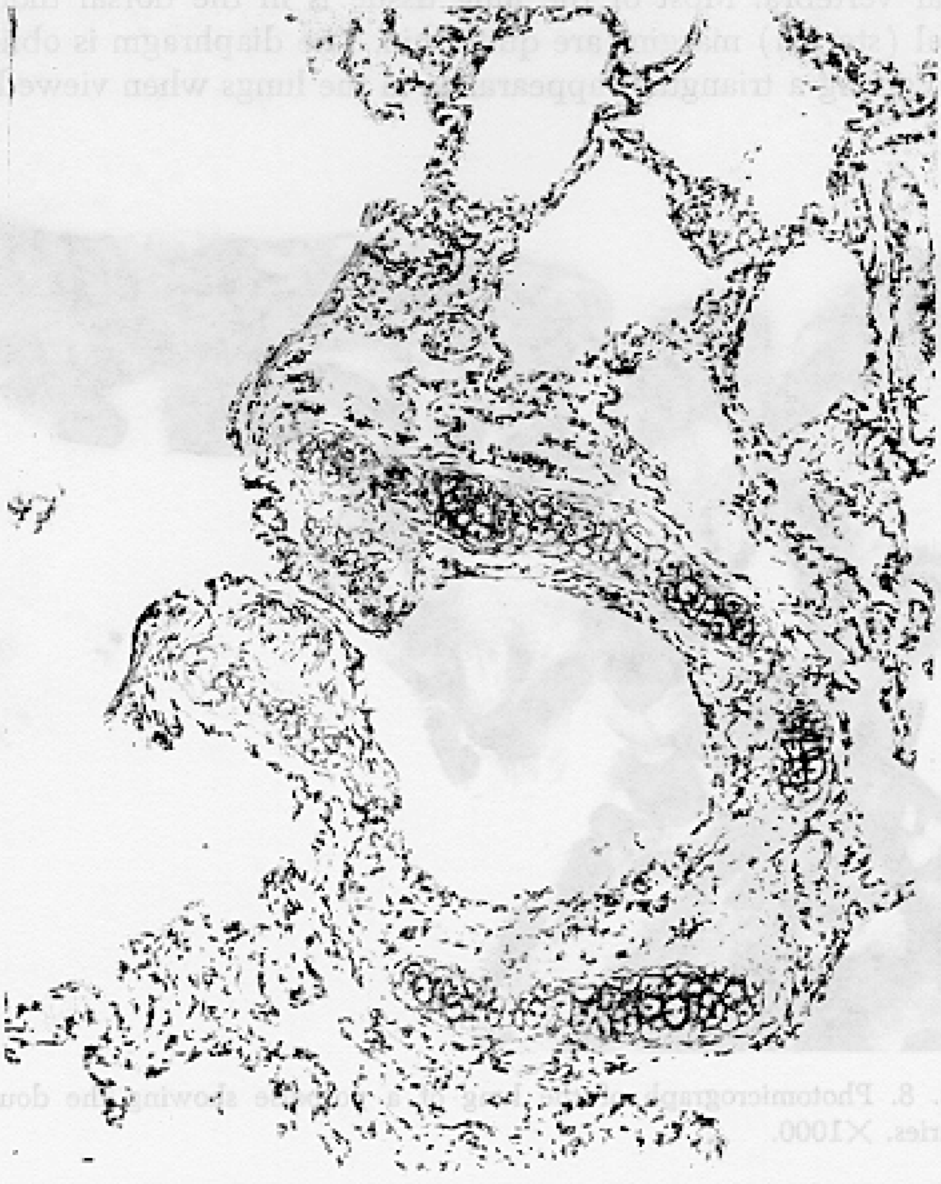

FIG. 7. Photomicrograph of *Tursiops* lung showing muscular sphincter. ×125.

cetaceans concerning the site where the two predominant types of sounds (whistles and click trains) are made. Some consider the larynx the site or origin of both types of sound, others argue that the sounds are produced by the air sacs along the nares, while still others contend that the whistles are produced in the larynx and the clicks in the air sacs and nares.

d. Trachea. The trachea is short because of the shortened neck, but large in diameter (robust) with numerous complete cartilage rings. Many of the heavy rings anastomose. This arrangement seems to provide for free and rapid movement of air.

e. Lungs. The lungs are large, elongated organs extending forward to 6–8 cm in front of the first ribs and as far posterior as the second or third lumbar vertebra. Most of the lung tissue is in the dorsal thorax as the ventral (sternal) margins are quite thin. The diaphragm is obliquely oriented, giving a triangular appearance to the lungs when viewed laterally.

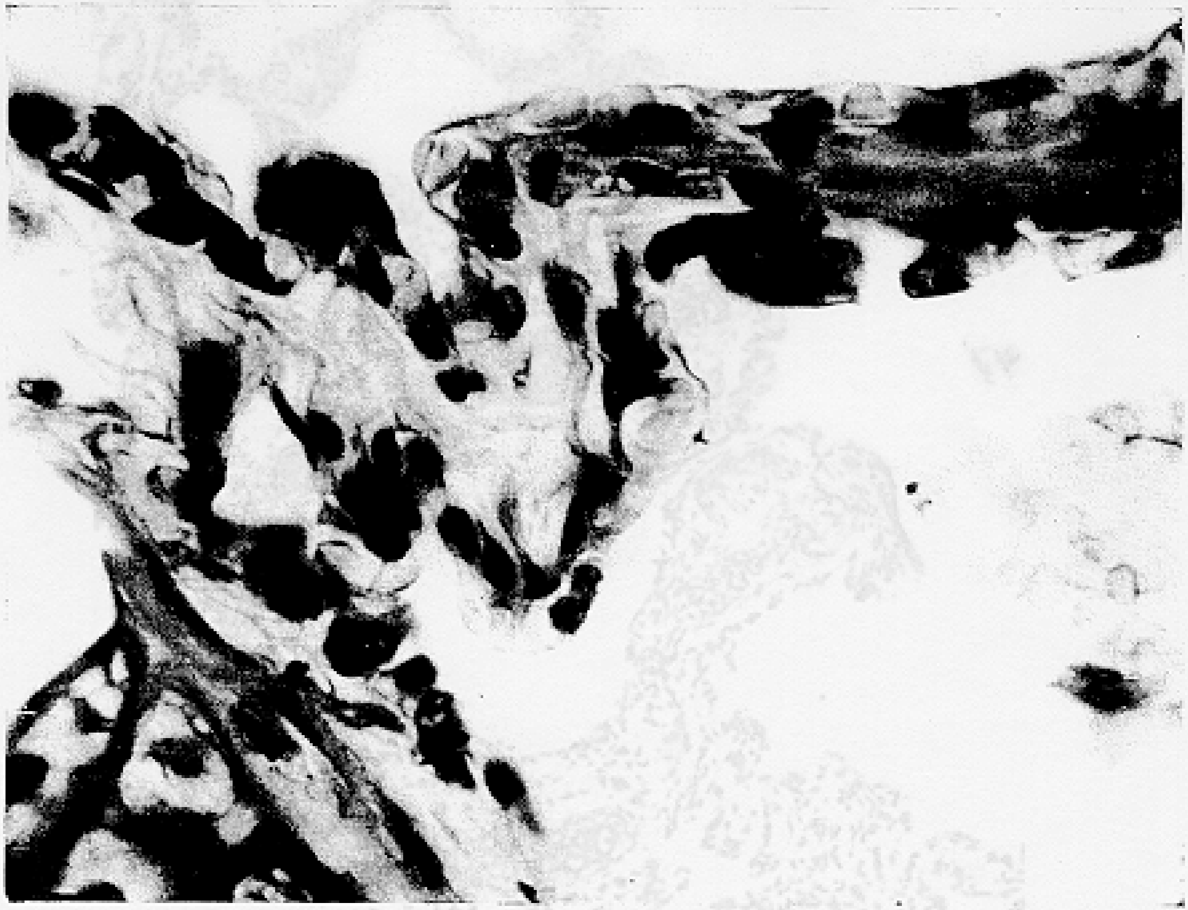

FIG. 8. Photomicrograph of the lung of a porpoise showing the double row of capillaries. ×1000.

The lungs show little to no external lobulation and are asymmetrical due in part to a separate right bronchus which branches about 5 cm above the bifurcation of the trachea into the two main bronchi.

The main bronchi, the stem bronchi, and the bronchioles are supported by an extensive network of cartilage rings which anastomose at irregular intervals. These cartilages produce a rigid bronchial tree, which aids in rapid, effective ventilation and resistance to pressure changes (Wislocki, 1929). The lungs as a whole are highly elastic, and the pleura are very thick and elastic as well. In each bronchiole, myoelastic valves produce

6–18 compartments. There are also muscular sphincters at the junction of the terminal bronchioles and the alveolar sacs (Fig. 7). The function of the sphincters is not clear, but Fiebiger (1916) theorized that they might function to keep air in the alveoli during diving. Scholander (1940), however, theorized that the alveoli collapse at depths of greater than 100 meters and that all the air is forced into the armored bronchial tree.

Another unique feature of the lungs is the presence of a sheet of elastic tissue which divides the septum between the alveoli (Fig. 8). This necessitates the development of a double capillary bed so that the alveolar capillaries are in contact with only one alveolus (Fiebiger, 1916). In other mammals there is a single layer of capillaries which are in contact with two alveoli. Gardner (1967) has recently investigated the structure of the lungs of some small cetaceans with the electron microscope. He made the somewhat surprising discovery that the alveolar wall in the pilot whale (*Globicephala scammoni*) is some 20 times as thick as that of most terrestrial mammals.

3. *The Cardiovascular System*

In *Tursiops* the heart represents a little better than 0.50% of body weight and is four-chambered, following the general mammalian plan. The ventricles contain a slightly greater number of trabeculae in comparison with most terrestrial mammals. For the purpose of brevity, only the four most marked deviations in circulatory anatomy from the mammalian norm (if there is such a thing) will be discussed. These modifications are no doubt related to the diving physiology of these mammals.

The most striking modifications in the anatomy of the circulatory system is seen in the peripheral vessels, especially the *retia mirabilia* (Fig. 9), which are spongy vascular masses found in various places throughout the body. The most extensive are the *thoracic retia* located on either side of the vertebral column and between the ribs. These retia extend forward into the lateral cervical region where they are called *cervical retia*. They also extend posteriorly into the lumbar region and on into the chevron (or hemal) canal. As may be seen in Fig. 9 the thoracic retia have an abundant nerve supply.

The retia are also found at the base of the brain and surrounding the optic nerve. There are other well developed retial networks in the spinal canal surrounding the spinal cord and in the sinuses of the head, especially around the ear bones.

Most cetacean retia have numerous highly elastic arterial branches, which anastomose among themselves. Those veins which are present are less elastic, have no valves, and contain no muscular tissue in their walls.

The retia have the capacity to hold much blood, so they may function as blood reservoirs, thereby acting to maintain steady blood flow to various critical areas of the body. These vascular networks are prominent near air-containing spaces such as the thorax and sinuses of the head, especially around the ear. Thus, they may function to a great extent as erectile tissue to alleviate pressure changes during diving. This function

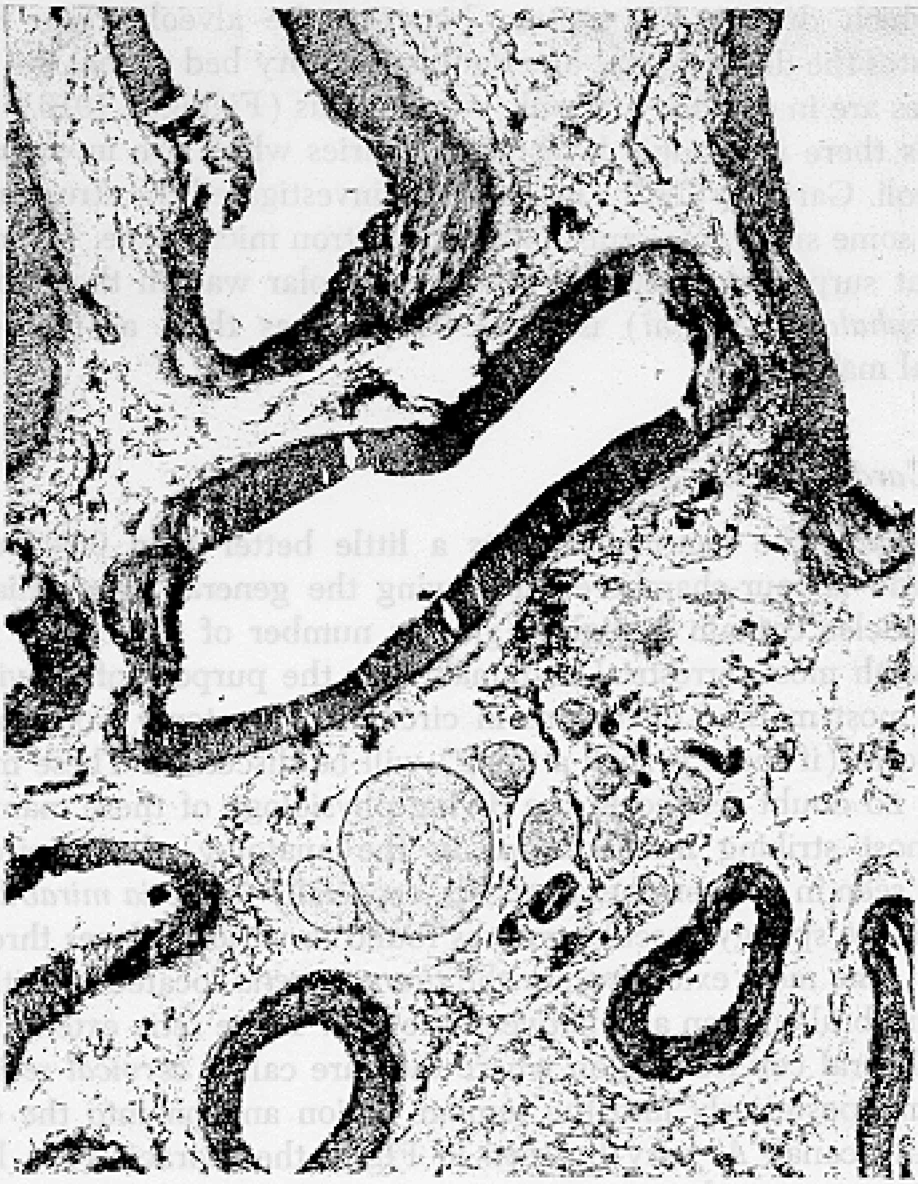

FIG. 9. Photomicrograph of the retia mirabilia. Note the large nerves. ×30.

has been proposed by Erickson (Scholander, 1940) for the cetaceans, and by Odend'hal and Poulter (1966) for the ear of pinnipeds.

There is in the flukes a system of subcutaneous veins generally paralleling the underlying fiber bundles. Deeper within the dense fibrous core there are dorsal and ventral arteries that give off numerous collaterals along their length. These arteries are surrounded by an extensive system of thin-walled veins (Fig. 10). It has been proposed (Scholander and Schevill, 1955) that this arrangement provides a countercurrent heat exchange mechanism whereby warm blood from the body passes through the arteries and yields up heat to the veins, where blood is flowing back to the interior rather than losing heat to the relatively cold water. There

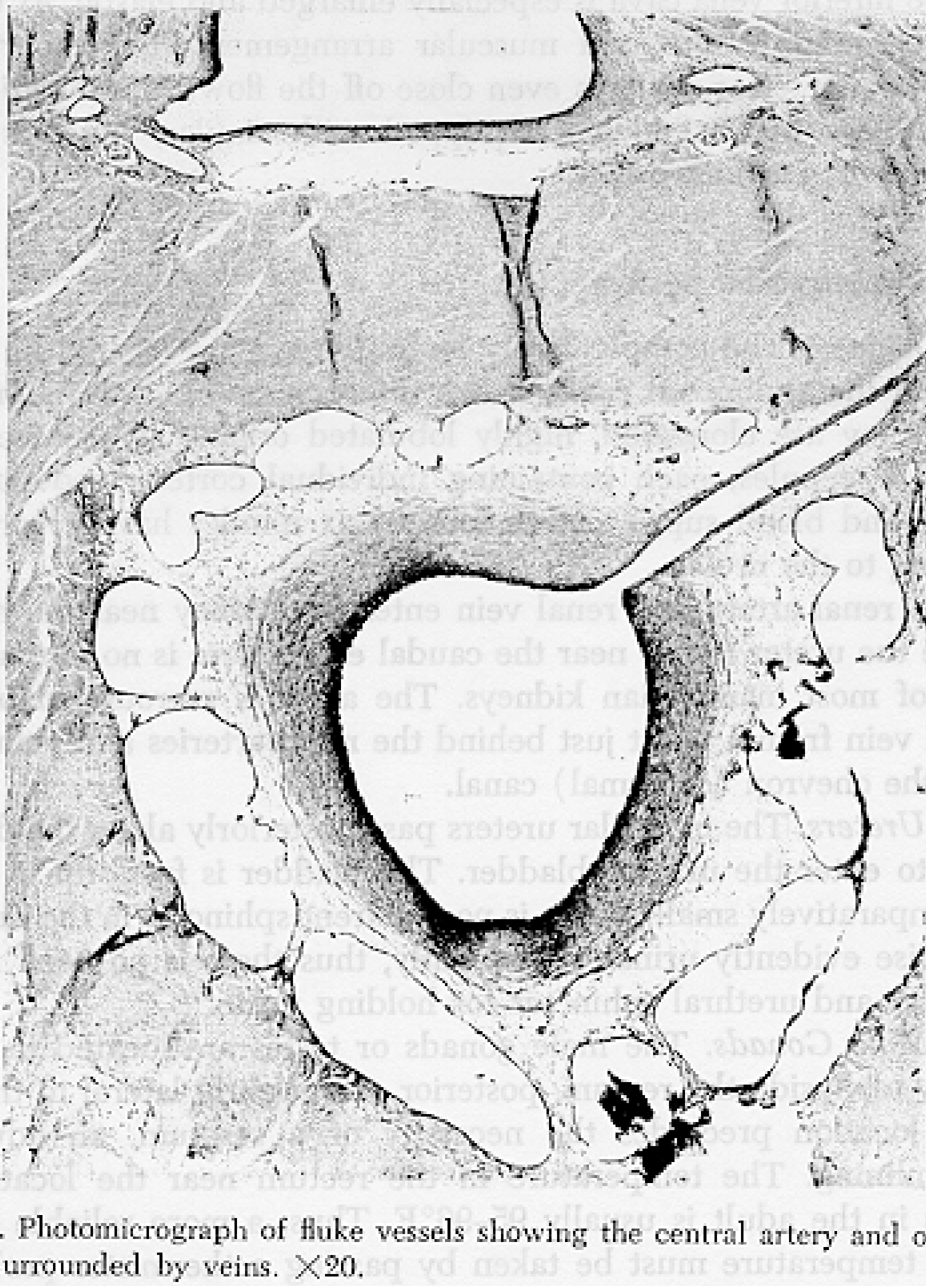

FIG. 10. Photomicrograph of fluke vessels showing the central artery and one of its branches surrounded by veins. ×20.

is a similar relationship between arteries and veins in the flippers, and in the dorsal fin, the main difference being that they lie deeper and more or less along a central distribution in the dorsal fin.

In the spinal canal just below the spinal cord and in the vascular network surrounding it there are two fairly large veins. These spinal veins are thought to be the principal route of circulation from the brain, the two jugulars being quite small. The spinal veins feed into the anterior vena cava in the thorax and into the posterior vena cava in the abdomen. Therefore, blood from the brain can return to the heart via the anterior vena cava or the posterior vena cava. These large spinal veins are devoid of valves and are apparently found in all aquatic mammals.

The inferior vena cava is especially enlarged and elastic. At the level of the diaphragm there is a muscular arrangement that can restrict this vessel diameter or perhaps even close off the flow. The hepatic veins are also highly distensible and equipped with similar, but less extensive, sphincterlike arrangements.

4. *The Urogenital System*

a. Kidney. The comparatively large kidneys are located on the dorsal wall of the abdominal cavity much the same as in other mammals (Fig. 11). They are elongated, highly lobulated organs. There are some 450 lobes or renules, each containing individual cortex, medulla, papillae, calyx, and blood supply. Each four to six renules have a common duct leading to the ureter.

The renal artery and renal vein enter the kidney near the rostral end, while the ureter leaves near the caudal end. There is no hilum characteristic of most mammalian kidneys. The aorta is surrounded by the post caval vein from a point just behind the renal arteries and veins posterior into the chevron (or hemal) canal.

b. Ureters. The muscular ureters pass posteriorly along the dorsal body wall to enter the urinary bladder. The bladder is fusiform in shape and is comparatively small. There is no apparent sphincter in the urethra. The porpoise evidently urinates frequently, thus there is no need for a large bladder and urethral sphincter for holding urine.

c. Male Gonads. The male gonads or testes are located in the pelvic cavity alongside the rectum, posterior and slightly lateral to the kidneys. This location precludes the necessity of a scrotum, an advantage in streamlining. The temperature in the rectum near the location of the testes in the adult is usually 95–96°F. Thus, a more reliable reading of body temperature must be taken by passing a thermister probe at least 25 cm into the rectum, where normal temperature is about 98.5°F. The epididymis is a narrow, elongated body extending from the rostral to the caudal end of each testis. The highly convoluted vas deferentia pass caudally to the colliculus seminalis, where they join the urethra. The prostate gland surrounds the proximal end of the urogenital canal. In some species of small toothed whales, notably *Lagenorhynchus obliquidens*, the Pacific white-striped porpoise, and *Delphinus delphis bairdi*,

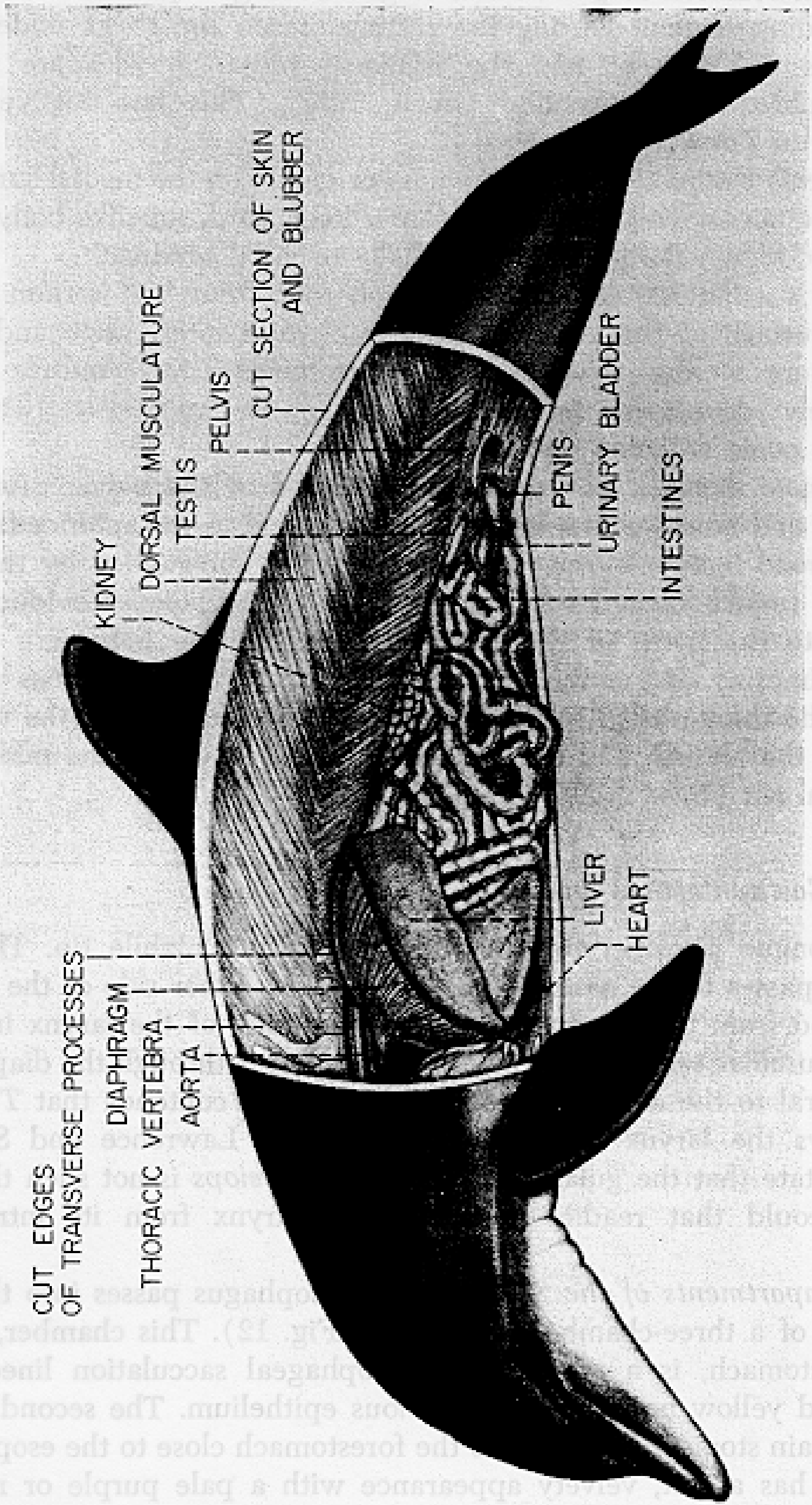

FIG. 11. Side view of *Tursiops* with abdominal wall cut away. The liver covers the stomach compartments in this view. (Drawn by Barbara Stolen from dissection by Robert F. Green.)

the Pacific common dolphin, the male goes through a period of rut during the breeding session. During the rutting season the testes undergo an enormous enlargement and the ischiocavernosal muscles are greatly hypertrophied (Ridgway and Green, 1967). This has not yet been observed in *Tursiops*, however.

The penis begins as two crura which originate on the medial surface of the pelvic bones. These arms fuse into a long, hard, ropelike body. From the pelvic region the penis runs cranially to the genital slit.

There is a flat retractor muscle which runs from its insertion on the ventral surface of the penis to the ligamentum intercrurale and rectal wall. There is also a well-developed ischiocavernosal muscle and a moderately developed bulbocavernosal muscle associated with the proximal penis (Slijper, 1958, 1966).

d. Female Gonads. The ovaries are located in the pelvic cavity just posterior and lateral to the kidneys and attached to the anterior free end of the broad ligament. Each ovary is partially surrounded by the wide fallopian funnel located on the distal end of the slender oviducts that connect to the horns of the bicornuate uterus. The horns are usually several times as long as the body of the uterus, which continues posteriorly to the thick-walled tubular vagina. The vaginal orifice, the urethral opening, the clitoris, and the anus are all housed within the midventral urogenital slit (Figs. 1 and 11).

5. *The Gastrointestinal System*

The tongue is rather robust, with a short but mobile tip. The oropharynx passes to the nasopharynx and around either side of the larynx. Thus food from the mouth passes on either side of the larynx into the highly muscular *esophagus*. The esophagus passes through the diaphragm just ventral to the aorta (Fig. 11). Lilly (1964) contends that *Tursiops* withdraws the larynx to swallow food, while Lawrence and Schevill (1965) state that the gular musculature in *Tursiops* is not such that the animal could that readily withdraw the larynx from its intranarial position.

a. Compartments of the Stomach. The esophagus passes into the first chamber of a three-chambered stomach (Fig. 12). This chamber, called the forestomach, is a nonglandular esophageal sacculation lined with white and yellow noncornified squamous epithelium. The second chamber, or main stomach, connects to the forestomach close to the esophageal end and has a soft, velvety appearance with a pale purple or maroon color. This chamber has thicker plicated walls containing fundic glands.

The main stomach passes into the pyloric or third stomach (sometimes called the connecting stomach) which has a velvety, reddish-brown lining containing numerous pyloric glands. This compartment leads by a narrow pyloric orifice to the much dilated ampulla of the duodenum, into which the large common bile duct empties.

b. The Intestines. The intestines are quite long, averaging about 30

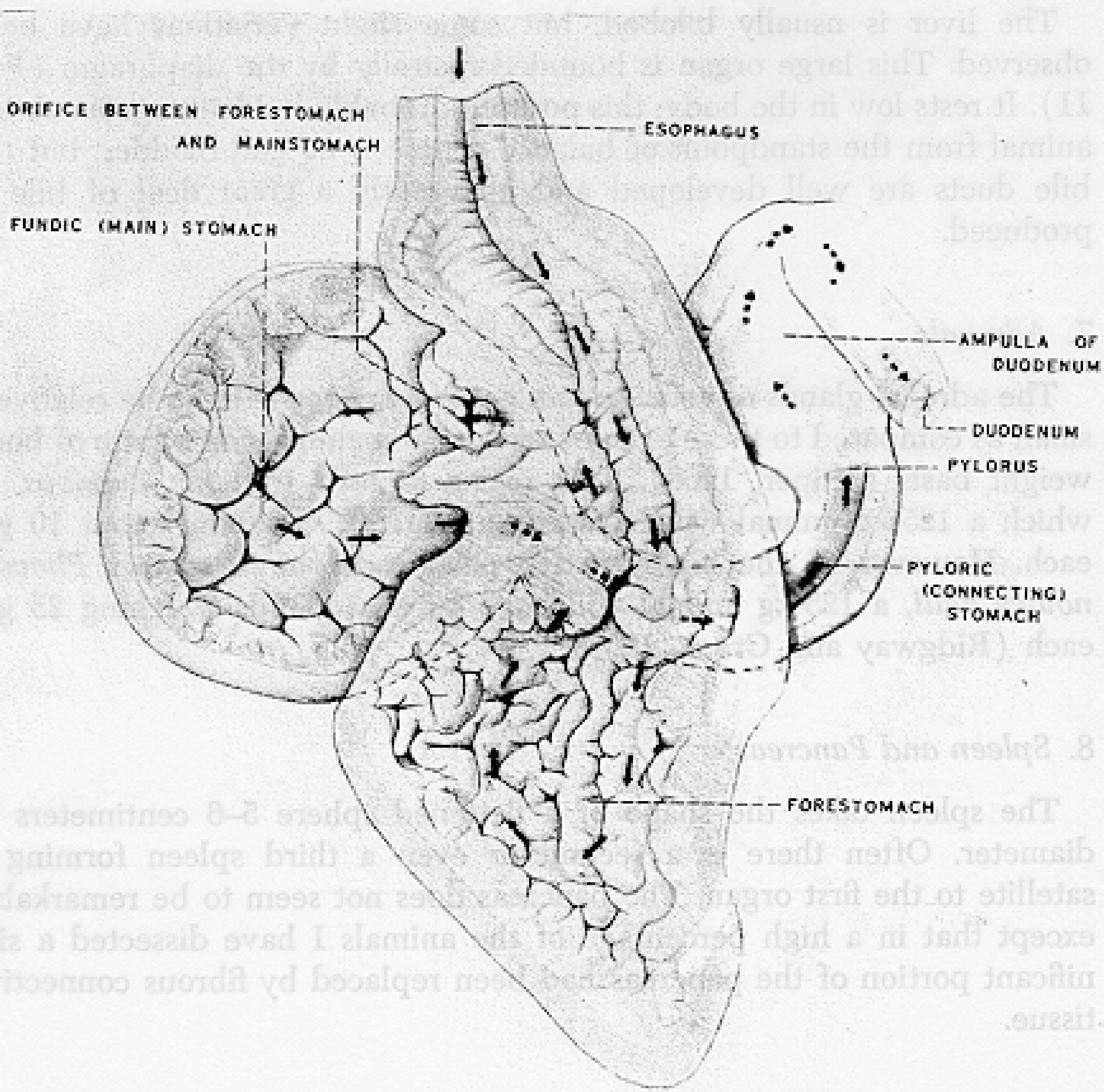

FIG. 12. Drawing of the stomach compartments of *Tursiops* with the dorsal portion of the forestomach and esophagus and main stomach cut away. The view is from above. (Drawn by Barbara Stolen from dissection by Robert F. Green.)

meters in an adult specimen. There is no cecum so that small intestine and large intestine cannot be differentiated grossly. Thus, it does not seem proper to designate a large and small intestine in these animals. Histologically (J. G. Simpson and Gardner, 1968) sections of the intestines appear similar from the termination of the duodenum to a point near the beginning of the rectum, where for a very short distance there is tissue which resembles that of the colon. The proximal duodenum is greater in diameter than any other part of the intestine.

6. *The Liver*

The liver is usually bilobed, but some slight variations have been observed. This large organ is bounded rostrally by the diaphragm (Fig. 11). It rests low in the body; this position probably is advantageous to the animal from the standpoint of balance. There is no gall bladder, but the bile ducts are well developed and apparently a great deal of bile is produced.

7. *Adrenals*

The adrenal glands of cetaceans in general are reported to be relatively small as compared to those of most terrestrial mammals on a ratio of body weight basis (Slijper, 1958). This seems to hold true for *Tursiops*, in which a 125-kg animal will have adrenal glands weighing about 10 gm each. However, in the highly active pelagic delphinid species *Phocoenoides dalli*, a 125-kg animal will have adrenal glands weighing 25 gm each (Ridgway and Green, 1968).

8. *Spleen and Pancreas*

The spleen takes the shape of a flattened sphere 5–6 centimeters in diameter. Often there is a second or even a third spleen forming a satellite to the first organ. The pancreas does not seem to be remarkable except that in a high percentage of the animals I have dissected a significant portion of the pancreas had been replaced by fibrous connective tissue.

9. *Organ Weights*

Specific data on organ weights in cetaceans is limited, but information gathered to date, on an interspecies basis, indicates a strong quantitative relationship between organ weights and morphological characteristics on the one hand and physiological and ecological characteristics on the other (Ridgway and Johnston, 1966; Ridgway and Green, 1968). Table I gives some average organ weights of *Tursiops truncatus* listed as percentage of body weight, and for a theoretical average 125-kg adult.

TABLE I
VALUES FOR ORGAN WEIGHTS EXPRESSED BOTH AS PERCENTAGE OF BODY WEIGHT AND AS AN ABSOLUTE WEIGHT FOR A THEORETICALLY AVERAGE 125-KG ANIMAL

Organ	(A)[a] Percentage of body weight	(B) Estimated organ weights for 125 kg theoretical porpoise	Remarks
Body weight	60–150 kg	125 kg	—
Heart	0.52	650 gm	—
Kidney	0.32 each kidney	375 gm	Left kidney sometimes slightly larger than the right
Adrenals	0.01 each adrenal	10 gm	—
Brain	1.70	1550 gm	Younger and smaller animals have higher brain weights relative to body weights
Liver	2.25	3000 gm	—
Pancreas	0.20	225 gm	—
Lungs	2.40 both	3100 gm	—
Spleen	—	50–100 gm	Spleen is extremely variable, depending often on cause of death
Thyroid	0.04	45 gm	—

[a] Data in column A were taken from both adult and immature animals and thus do not necessarily relate mathematically to column B. A 125-kg *Tursiops* is usually mature or nearing maturity.

10. *Cytogenetics*

The results of cytogenetic studies on *Tursiops truncatus,* male and female, have recently been reported (Walen and Madin, 1965; Duffield *et al.,* 1967). *Tursiops truncatus* has a diploid chromosome number of 44. These chromosomes can be arranged by pairs into groupings as represented in Fig. 13. All chromosome pairs in groups A and B are submetacentric, the centromere of each chromosome lying at any point between the middle and tip of the chromosome. Those of group C are metacentric, the centromere medial in position. Group D consists of acrocentric pairs, the centromere being located near the tip of the chromosome. Within these groups, the chromosome pairs are arranged by size and can be identified as A-1 through A-5, B-6 through B-12, C-13 through C-16, and D-17 through D-21. The last pair represents the sex chromosome. The Y chromosome is the smallest of the entire complement; the X chromosome a metacentric very nearly the size of B-11.

11. *The Ear*

The external auditory meatus terminates at the tympanic annulus in the lateral surface of the tympanic bulla. The bulla forms the ventral as well as part of the lateral and medial walls of the tympanic cavity housing the middle ear.

The tympanic membrane consists of two parts, the fibroligamentous portion and a smaller nonfibrous portion. The ligamentous part, which is considered homologous to the fibrous tympanic membrane in terrestrial mammals attaches distally to the *malleus*.

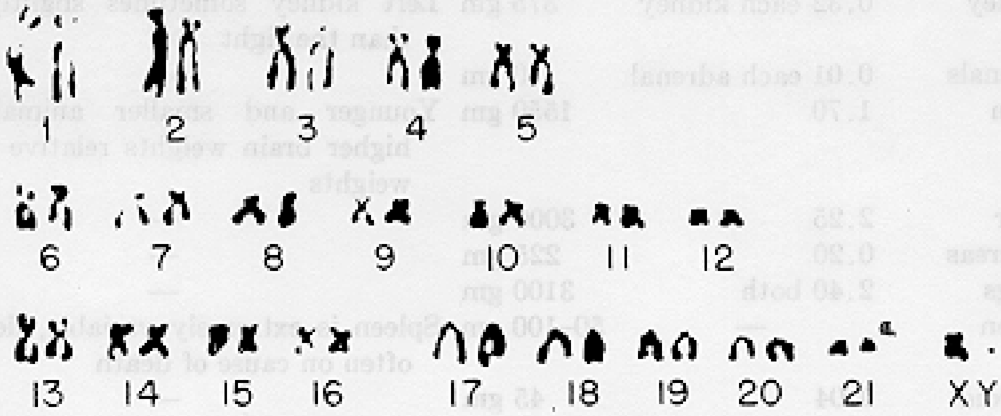

FIG. 13. Chromosomes of a male *Tursiops*.

The *malleus* articulates with the *incus* which in turn articulates with the *stapes*. The foot of the *stapes* fits into the fenestra ovale.

In addition to the tympanic bulla, the tympanic cavity is bounded dorsally by the *periotic* bone, which, as in most cetaceans, is dissociated from the rest of the skull (Purves and Van Utrecht, 1963). The *tympano-periotic* bone is surrounded by a highly vascular system of air sinuses. These sinuses also invade the tympanic cavity as well as extend forward along the ventral surface of the rostrum.

The blood flow to the tympanic cavity and the corpus cavernosum tympanum is by way of the highly reduced internal carotid artery. The blood supply to the fibrovenous plexus of the peribullary air sacs is by numerous small branches of the maxillary artery. Drainage of the middle ear is mainly by transverse and cavernous sinuses of the cranium while the venous plexus of the air sacs are drained by vessels feeding into the spinal meningeal veins, the external jugular veins, and the mandibular veins.

This extensive vascular network completely surrounds all the osseous structure of the ear (Fig. 14) and makes surgical procedures on the ear very difficult. Recently, cochlear potentials were successfully recorded from the ears of bottlenose porpoises at Princeton University's Auditory Research Laboratory (McCormick *et al.*, 1968). However, the surgical procedures required 4–7 hours whereas in most terrestrial mammals this operation can be accomplished in 1 hour or less.

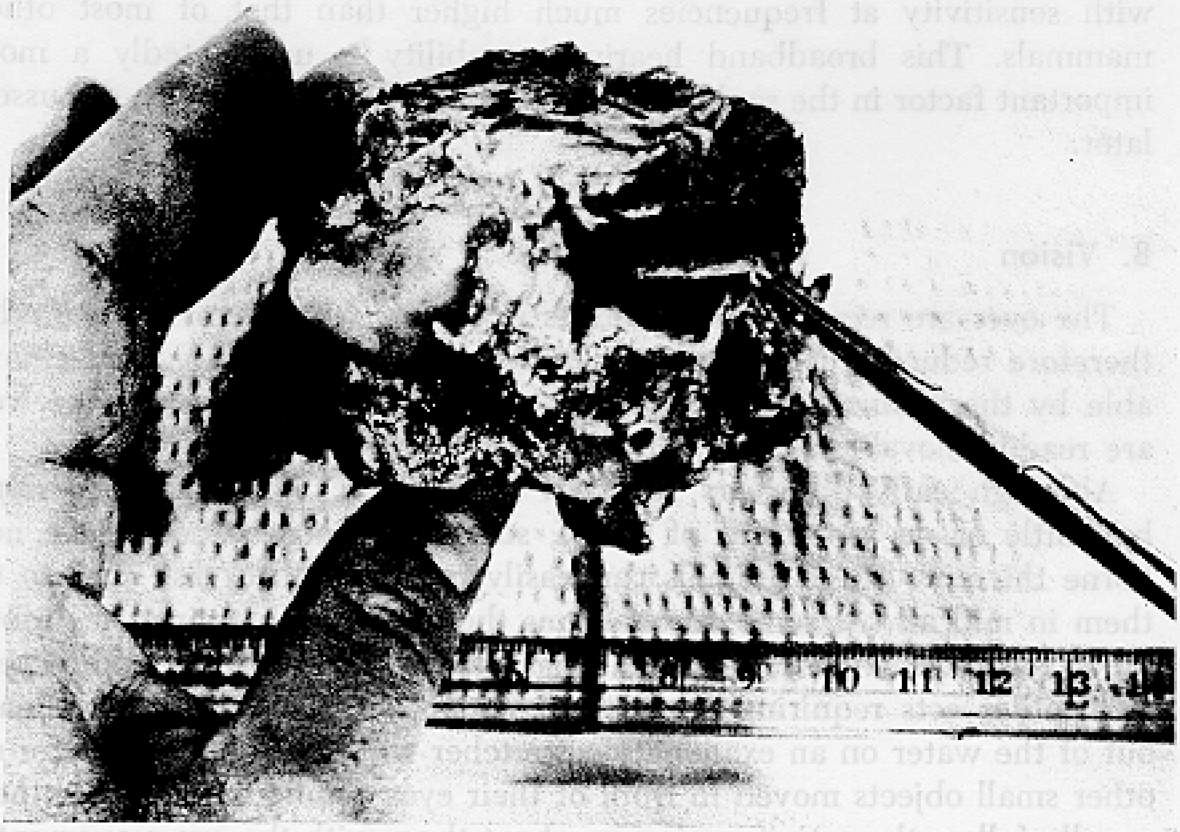

FIG. 14. The ear bones of *Tursiops* showing the vascular networks. The corpus cavernosum is grasped by the forceps.

The *eustachian tubes* pass from the air sacs just anterior to the tympanoperiotic bones forward along the basioccipital crest and into the nasopharynx.

III. Senses

A. Hearing

As mentioned earlier the auditory nerve is the largest of the twelve cranial nerves. Most investigators who have worked with *Tursiops* have quickly come to the conclusion that audition is the most prominent sense in this species. Thus, the porpoise lives in a world of sound just as it may be said that the dog lives in a world of smell. Johnson (1966) used operant conditioning to train a bottlenose porpoise to respond to pure tone signals. He thus obtained an audiogram over the frequency range of 75 Hertz to 150 kHz. The greatest hearing sensitivity occurred in the frequencies near 50 kHz at a level of about −55 decibels (reference 1 microbar). The effective upper limit for Johnson's experimental animal was determined to be 150 kHz. Thus, *Tursiops* has broadband hearing with sensitivity at frequencies much higher than that of most other mammals. This broadband hearing capability is undoubtedly a most important factor in the sophisticated sonar system which will be discussed later.

B. Vision

The eyes are recessed in the orbits in such a way as not to protrude, therefore reducing drag. Both the upper and lower lids are freely movable by the sphincterlike orbicularis oculi muscle. The eyes themselves are readily movable as well. There are no eyelashes.

Although early observers reported (Townsend, 1918) that *Tursiops* had little or no vision out of water; subsequent observations have not borne this out. These animals can easily catch a ball or fish thrown to them in mid air. At some oceanariums they have been trained to throw fairly accurately a basketball into a basket, using the rostrum, and to perform other acts requiring fairly good visual acuity in air. Also animals out of the water on an examination stretcher will often follow a finger or other small objects moved in front of their eyes. While out of water they usually follow the activity going on about them with the eye movements. At least one animal learned to urinate when it saw urethral catheters.

C. Tactile Senses

Not a great deal can be said about the sense of touch in porpoises from an experimental point of view. From general observations it would appear that tactile senses are fairly well developed. The skin is well endowed with nervous innervation. Porpoises are sensitive to pin or needle pricks to the skin anywhere on the body. They seem particularly sensitive to being touched with a hot object. Some trained animals appear to enjoy being stroked or petted by their trainers. They also seem to enjoy body contact with one another and especially during sexual play they will rub bodies and stroke each other with flippers, flukes, or the tail stock.

The vestigial whiskers, mentioned earlier, along the dorsum of each side of the rostrum may also function as tactile sensory receptors. These recessed pits contain the remains of a hair (Fig. 3), and a good blood and nerve supply is present.

D. Olfaction and Taste

The brain of *Tursiops* does not have olfactory bulbs ~~lobes~~, and this, together with the arrangements of the nares, would seem to indicate that the sense of smell is lacking. The gustatory sense is reported to be lacking, but rudimentary taste buds have been described (Slijper, 1958). Many who have observed the behavior of these animals, and especially those who have trained them, would disagree with the report that the sense of taste is absent based upon the fact that bottlenose porpoises are often very selective about their food.

Jablokov and Belkovitsh (1962) proposed that cetaceans have chemoceptors in the depressions found at the base of the tongue. However, I am not aware of any experimental evidence that would elucidate the situation concerning the gustatory and olfactory senses in these animals.

IV. Physiology

A. Respiration and Diving

Adult *Tursiops* breathe two to three times per minute. Each breath is a deep one, and tidal air is about 80% of lung capacity. Irving *et al.* (1941) determined that the respiratory volume varied from 5 to 10 liters in adult specimens. The blood oxygen dissociation curve is to the left of that of man and pig, but to the right of that of some other small toothed whales (Horvath *et al.*, 1968). Porpoises usually hyperventilate before a deep or prolonged dive, taking four or five rapid breaths.

These porpoises are relatively poor divers as compared to some other cetaceans: the bottlenose whale (*Hyperoodon rostratus*) reportedly can dive for 2 hours (Scholander, 1940), and the sperm whale can dive for 1½ hours and can probably attain depths of more than 1000 meters (Heezen, 1958). There are three reports of voluntary dives of *Tursiops truncatus* lasting from 4½ minutes to 7 minutes and 15 seconds (Irving *et al.*, 1941; Ridgway, 1966; Elsner *et al.*, 1966). A trained bottlenose porpoise made dives to 170 meters depth (Ridgway, 1966).

B. Osmoregulation

The problem of water balance in marine mammals has been one of particular interest. The blood of *Tursiops* is only slightly higher in salinity than that of man (Eichelberger *et al.*, 1940; Medway and Geraci, 1965; Ridgway, 1965; Ridgway *et al.*, 1968). As far as is known cetaceans lack any special cells for removing salts as seen in fishes and certain birds.

Thus porpoises must maintain water balance in seawater, which is considerably higher in salinity than their own blood and body fluids. The cetaceans that feed primarily on fish, such as *Tursiops*, have a diet high in fat. Thus a high oxidation rate of food and a high fat intake would yield a great deal of metabolic water. Fetcher and Fetcher (1942), Krogh (1939), and Lilly (1964) have made calculations which show that *Tursiops* can meet all its water requirements through the fish that it consumes. Fetcher and Fetcher (1942) have provided some experimental evidence that *Tursiops* cannot process seawater. Lilly (1964) contends that bottlenose porpoises do not swallow seawater, claiming that each fish that the animal eats is squeegeed free of seawater by muscles in the throat.

Recently my associates and I carried out some experiments in an attempt to learn whether or not these animals swallowed seawater. Two apparently healthy adult porpoises, one male and one female, were placed in a freshwater pool for 48 hours, then returned to the usual seawater environment. Blood and urine samples were collected for electrolyte and osmolarity determinations just before the animals were placed in freshwater, 24 hours after being placed in freshwater, 48 hours after being placed in freshwater, and 24 hours after being returned to the seawater pools. During the first 24 hours in freshwater the animals were fasted, during the second 24 hours in freshwater they were fed 6 and 8 kg, respectively, of Pacific mackerel (*Pneumatophorus diego*) which contains 90–100 mEq/l sodium. Table II gives the results.

TABLE II

URINE ELECTROLYTE VALUES FOR TWO *Tursiops* THAT WERE MAINTAINED IN FRESHWATER FOR 48 HOURS AND THEN PLACED INTO SEAWATER

	Animal A, female *Tursiops*, 165 kg			Animal B, male *Tursiops*, 123 kg		
	Sodium	Potassium	Chloride	Sodium	Potassium	Chloride
Removed from seawater	376	70.0	308	91	86	242
End of 1st 24 hours (freshwater; fasted)	4.0	34.0	38	10	44	42
End of 2nd 24 hours (freshwater; fed)[a]	8.5	71	16.5	17	42	26
End of 3rd 24 hours (seawater; fasted)	365	68	496	82	72	276

[a] During second 24-hour period in freshwater, animal A was fed 8 kg of mackerel and animal B was fed 6 kg of mackerel.

The blood values during the two 24-hour periods in freshwater did not vary significantly from those taken when the animals were in seawater. The urine osmolality dropped while the animals were in freshwater, but the serum osmolality remained unchanged. The rapid rise of the urine electrolytes to or above pretest levels at the end of the third 24-hour period seems to indicate that the animals took in seawater.

Work is still underway on the problems of osmotic regulation in marine mammals. Animals which eat squid have a diet that is isosmotic with seawater, and the mechanism of their water economy has not been fully elucidated. The same situation as applied to lactating females and animals that appear to fast for long periods has not been explained.

C. Thermoregulation

Maintaining a mammalian body temperature (about 98.5°F for *Tursiops*) in relatively cold waters that conduct heat very rapidly is another unique problem of marine mammals. This problem is dealt with by cetaceans in three ways: a high metabolic rate, a countercurrent heat exchange system in the peripheral blood vessels (Fig. 10), and an insulating layer of blubber. Kanwisher and Sundnes (1966) have reported on the physiology of *Phocaena phocaena*, a very small porpoise that lives in very cold waters. Its metabolic rate is three times higher than that for other

TABLE III

SOME PHYSIOLOGICAL VALUES FOR A THEORETICALLY AVERAGE ADULT *Tursiops*

1. Respiratory rate, 2–3/min	17. Serum osmolarity (milliosmoles/l) (freezing point technique), 330
2. Rectal temperature, 98.5°F	18. Heart rate, 50–120
3. PCV, 45%	19. Hemoglobin (gm/100 ml), 14.4
4. Cholesterol (mg/100 ml) (Bloor's method), 200	20. Blood glucose (mg/100 ml) (modified Folin-w/v method), 120
5. Blood volume (ml/kg) (I^{131} dilution technique), 71	21. Blood urea nitrogen (mg/100 ml) (phenate-hypochlorite method), 40
6. Serum sodium (mEq/l), 150	22. Blood pH, 7.35
7. Serum potassium (mEq/l), 4.0	23. Blood oxygen (partial pressure, mm Hg), 95
8. Serum chloride (mEq/l), 110	24. Blood carbon dioxide (partial pressure, mm Hg), 45
9. Urine albumin, negative	25. Total white blood cells/mm², 9000
10. Urine sugar, negative	26. Neutrophiles (%), 60
11. Urine pH, acid	27. Eosinophiles (%), 15
12. Urine sodium (mEq/l), 200	28. Basophiles (%), 0
13. Urine chloride (mEq/l), 250	29. Lymphocytes (%), 20
14. Urine potassium (mEq/l), 80	30. Monocytes (%), 5
15. Urine specific gravity, 1.020–1.055	
16. Circulation time, fluke to tongue (I^{131} technique), 13 seconds	

mammals of its size, and its blubber represents about 40% of its body weight. Another larger porpoise (*Phocoenoides dalli*), which lives in very cold waters has handled the problem primarily by an increase in metabolic rate, since it has extremely thin blubber (Ridgway and Johnston, 1966). *Tursiops* is larger and lives in relatively warm waters; thus it does not require either the greatly increased metabolic rate or nearly as much insulation as does *Phocaena*. The large thyroid (Table I) and relatively high food consumption, however, indicate that *Tursiops* does have a higher metabolic rate than a terrestrial mammal of comparable size.

D. Basic Physiological Values

Table III gives some basic physiological values for a theoretically average adult *Tursiops truncatus*. These values are taken from Ridgway (1965), Ridgway and Johnston (1966), and Ridgway *et al.* (1968). Medway and Geraci (1965; Medway *et al.*, 1966) have also reported on the hematology and blood chemistry of bottlenose porpoises.

1. *Blood Clotting Times*

Clotting times measured by the Lee and White method have always been prolonged. They range from 30 to 60 minutes, 45 minutes being an approximate average. If the blood is contaminated with seawater, the clotting time is much more rapid. It has been observed that clot retraction, under normal conditions, does not begin to occur up to 24 hours after blood is drawn.

2. *The Electrocardiogram*

In *Tursiops* there is a normal respiratory cardiac arrythmia whether the animal is swimming or resting out of the water. Within about 1 second after inspiration the heart rate increases to around 120 beats per minute and then slows as the period of apnea increases. Just before the next breath the heart rate will be 30–60 beats per minute. Thus, the heart rate slows and speeds up in a cyclic fashion with respiration. Irving *et al.* (1941) first reported this phenomenon in *Tursiops*, and Kanwisher and Sundnes (1966) observed it in *Phocaena*. I have also observed the same cardiac arrythmia in at least five other species of small toothed whales. The cardiac arrythmia usually is not manifested if the animal is excited, as just after capture. Several drugs that depress the central nervous system also eliminate the normal cardiac arrythmia.

For electrocardiograms we have standardized lead placements with the left arm lead at the left axilla, the right arm lead at the right axilla, and the chest lead at the center of the dorsum of the thorax along the same plane as the other two leads, since the animal is usually resting on its underside. When compared to normal human electrocardiograms the tracings are similar except that *Tursiops* exhibits a slightly increased P-R interval and an inverted or biphasic T wave. Flat plate or needle electrodes may be employed. The skin resistance in *Tursiops* usually ranges from 100 to 1200 ohms, a much lower skin resistance than in man. Thus, good electrocardiograms, without base line drift, can easily be obtained with contact electrodes.

V. Clinical Procedures

A. Blood Collection

Blood for analysis is drawn from the central veins or arteries of the tail flukes (Fig. 15). The flipper can be used equally well (Medway and Geraci, 1964). The central artery of the tail fluke is surrounded by a venous plexus (Fig. 10). If the artery is penetrated, which often occurs, a mixed venous or arterial sample may be taken even though the needle is in one of the veins. If an arterial blood sample is desired the veins are punctured and the needle is slowly advanced into the artery.

B. Urine Collection

Urine specimens are collected by catheterization. In the female the urethral orifice lies just below the clitoris and is of adequate diameter so that a No. 10–14 French catheter is usually easily passed. However, since the penis of the male contains a sigmoid flexure, a 20-inch No. 6 or 8 French canine catheter seems to be best.

C. Body Temperature

Rectal temperature should be measured by the use of a thermistor probe passed about 25 cm into the rectum. The temperature at this depth is normally about 98.5°F. The clinical glass thermometer is not safe for use in porpoises because it may break if the animal swings its tail. In addition, the temperature at a depth of 6–10 cm, where clinical glass thermometers normally measure it, usually varies from 93 to 97°F.

D. Injections

Intramuscular injections may be made in the abdominal muscles or in the dorsal musculature on either side of the dorsal fin. A needle at least 1½ inches in length should be employed to be sure the muscle is penetrated, and no more than 5 ml should be injected in any one site. Intravenous injections can be made into the central veins of the tail fluke or flipper.

FIG. 15. Drawing blood from the central vessels of the tail flukes.

E. Oral Medication

If the porpoise is eating, medication may be placed in food fish (Fig. 16). If the animal is off feed, an equine colt stomach tube may be employed. The tube can be passed from 65 cm to 1 meter in from the angle of gape, depending upon the size of the animal. Because of the intranarial position of the larynx, there is little danger that the tube will be passed into the trachea.

F. Anesthesia Procedures

The same physiological and anatomical characteristics which have resulted from the marvelous adaptation of cetaceans to aquatic life have made the problem of producing safe, but effective, surgical anesthesia a challenging one. Apneustic breathing, apparently complicated central nervous system respiratory control, specialized thermoregulation, and structure and functioning of the larynx have necessitated unique equipment and procedures.

1. *Sleep*

Behavior of porpoises during natural sleep has been discussed by Lilly (1964), McBride and Hebb (1948), and McCormick (1967). Lilly (1964) proposed that inhibition of respiration takes place at a thalamocortical level. He further proposed that only one-half of the brain sleeps at any one time, allowing the animal to actively surface under conscious volition for each breath during sleep periods. McCormick (1967), however, has made extensive observations of sleep behavior in *Tursiops* and reports two types of sleep. McCormick has observed a passive surface sleep which was also described by McBride and Hebb (1948). During this type of sleep the porpoise usually hangs near the surface with the trunk of the body nearly parallel to the surface and the tail dangling down. Both eyes are closed. In the absence of water current the animal rests almost motionless. About twice each minute the tail will stroke slowly lifting the animal to the surface for a breath. Long periods of sleep (as long as 1 hour) were always of the surface sleep variety. A second type of sleep referred to as "bottom sleep" or "cat napping" is also described by McCormick (1967). In this case the animal rests near or on the bottom coming up periodically to breathe. These periods of napping on the bottom may last as long as 4 minutes before the animal comes to the surface to breathe, after which it may or may not resume the nap. Tomilin (1957) attributes the porpoise's surface-sleep respiration to a reflex mechanism involving the tail flukes.

I have observed both types of sleep described by McCormick (1967). I also feel, based on my observations of animals in natural sleep and during anesthesia, that the stroking of the tail fluke is intimately tied in with respiratory control. It will no doubt be necessary to obtain considerable neurophysiological data before the complicated central nervous system control of respiration will be fully understood.

2. *Early Anesthesia Attempts*

The first attempt to anesthetize a porpoise was made by Langworthy (1932), who employed ether administered by a cone over the blowhole. The porpoise did not survive. In 1955 a group of workers attempted to

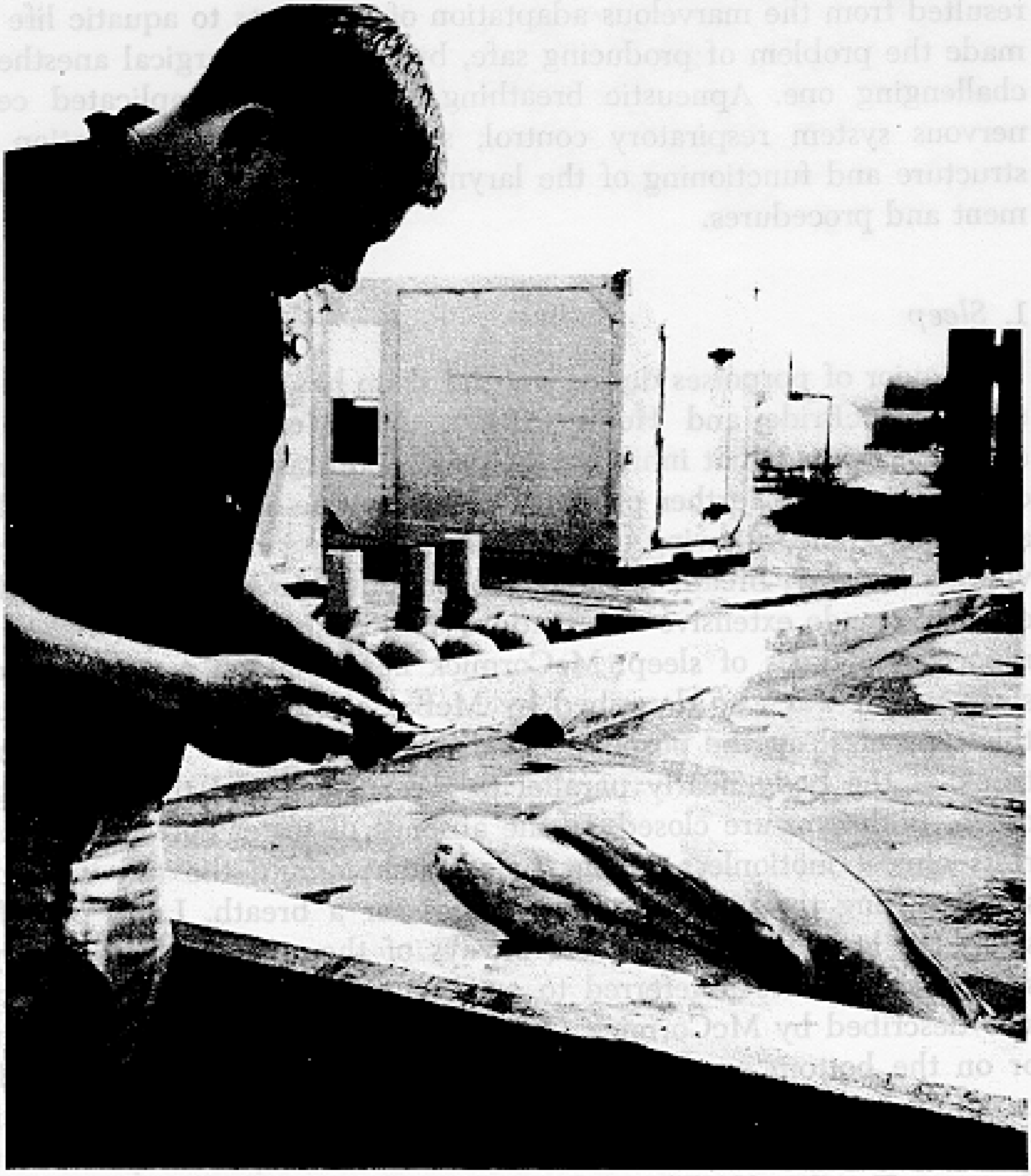

FIG. 16. Attendant places a vitamin capsule in a fish as a porpoise looks on.

use pentobarbital anesthesia for comparative electroneurological recordings on the porpoise brain. These observations were later reported by Lilly (1962). These investigators were unable to perform venipunctures, so they administered the pentobarbital intraperitoneally. The dosages for a series of five animals ranged from 30 to 10 mg/kg; in each case there was loss of respiratory control before other signs of anesthesia, and all the animals died.

3. *Affect of Thiopental Sodium on Respiration*

Prior to our experiments with assisted respiration (Ridgway, 1965; Ridgway and McCormick, 1967), I administered euthanasia to three Pacific white striped porpoises, *Lagenorhynchus obliquidens*, employing intravenous thiopental sodium. The animals were instrumented for monitoring of the electrocardiogram before the barbiturates were given. The intravenous thiopental sodium produced almost immediate anesthesia with loss of reflexes in a manner similar to that seen in the dog. After injection of only a portion of the dose (roughly 6 mg/kg) the animal seemed to lose control of the blowhole. The barbiturate was given to effect until the lid and gag reflexes were lost (15–25 mg/kg were required). The heart rate was rapid, 140–160 beats per minute, but steady. The cyclic rhythm of the heart beat mentioned before (respiratory arrhythmia) disappeared rapidly. About 5 minutes after administration of the barbiturate, the mucous membranes of the buccal cavity were extremely cyanotic and the heart rate began to decrease. Seven to 10 minutes after administration of the thiopental the heart stopped. None of these animals took a breath after the barbiturate was administered. It was amply apparent that in these three cases, death resulted solely from asphyxia.

4. *The Bird Respirator with Apneustic Plateau Control*

In 1964, Dr. Forrest Bird of the Bird Corporation, Palm Springs, California, developed an apneustic plateau control unit compatible with the Bird Mark 9 large-animal respirator. This unit effectively imitates the natural respiration of the porpoise in inflating the lungs rapidly, holding an apneustic plateau for a variable period and then deflating the lungs and rapidly filling them again.

5. *Anesthesia Attempts with Assisted Respiration*

Nagel *et al.* (1964) employed the Bird equipment in an attempt to produce barbiturate anesthesia in a porpoise. These investigators gave 13 mg/kg of thiopental sodium and 5 mg/kg of methohexital intraperitoneally. This experiment resulted in an anesthetic death. In the same report a technique of employing 50–70% nitrous oxide for anesthesia was outlined. Later Nagel *et al.* (1966) reported the use of nitrous oxide supplemented with succinyldicholine as an anesthetic preparation for major surgery in porpoises. Nitrous oxide has been employed in our laboratory, and I feel that it is inadequate for surgical anesthesia in porpoises (Ridgway, 1965; Ridgway and McCormick, 1967), halothane being preferable.

6. *Halothane Anesthesia Procedure*

Halothane has been employed successfully as an anesthetic agent for both experimental and clinical surgical procedures (Ridgway, 1965;

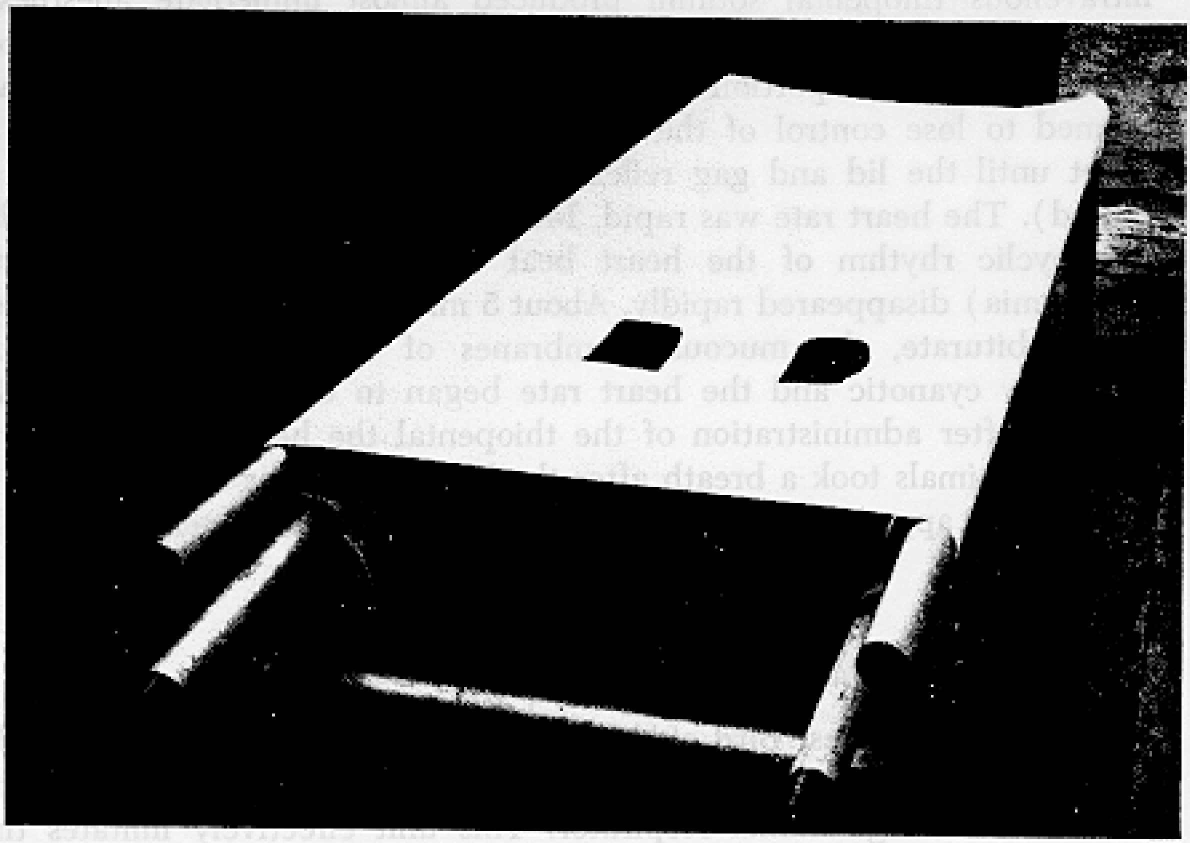

FIG. 17. Stretcher used for examination and surgery. Note the holes that accommodate the flippers. If abdominal surgery is to be performed, a hole is placed in the center for the dorsal fin.

Ridgway and McCormick, 1967). The following procedure is now employed in our laboratory for anesthetization of porpoises for major surgery.

The animal is taken from the water and placed on a specially constructed stretcher (Fig. 17). Five standard automobile seat belts are passed around the animal and adjusted snugly to provide restraint. The animal, secured to the stretcher, is taken into the surgery room and placed on a table which can be tilted in any direction, and which has provisions for drainage of water used to keep the animal moist and cool

(Fig. 18). Instrumentation leads are attached, and physiological monitoring is started. The rectal temperature is monitored by a YSI telethermometer thermistor probe inserted at least 20 cm into the rectum. pO_2, pCO_2, and pH in blood, collected from central arteries and veins in the tail flukes approximately every 5 minutes, are measured with an expanded scale pH meter using O_2 and CO_2 electrodes (Instrumentation Laboratory, Inc. macrosample models 123 and 125-A). Oxygen in the inspired and expired air is measured with a paramagnetic oxygen analyzer

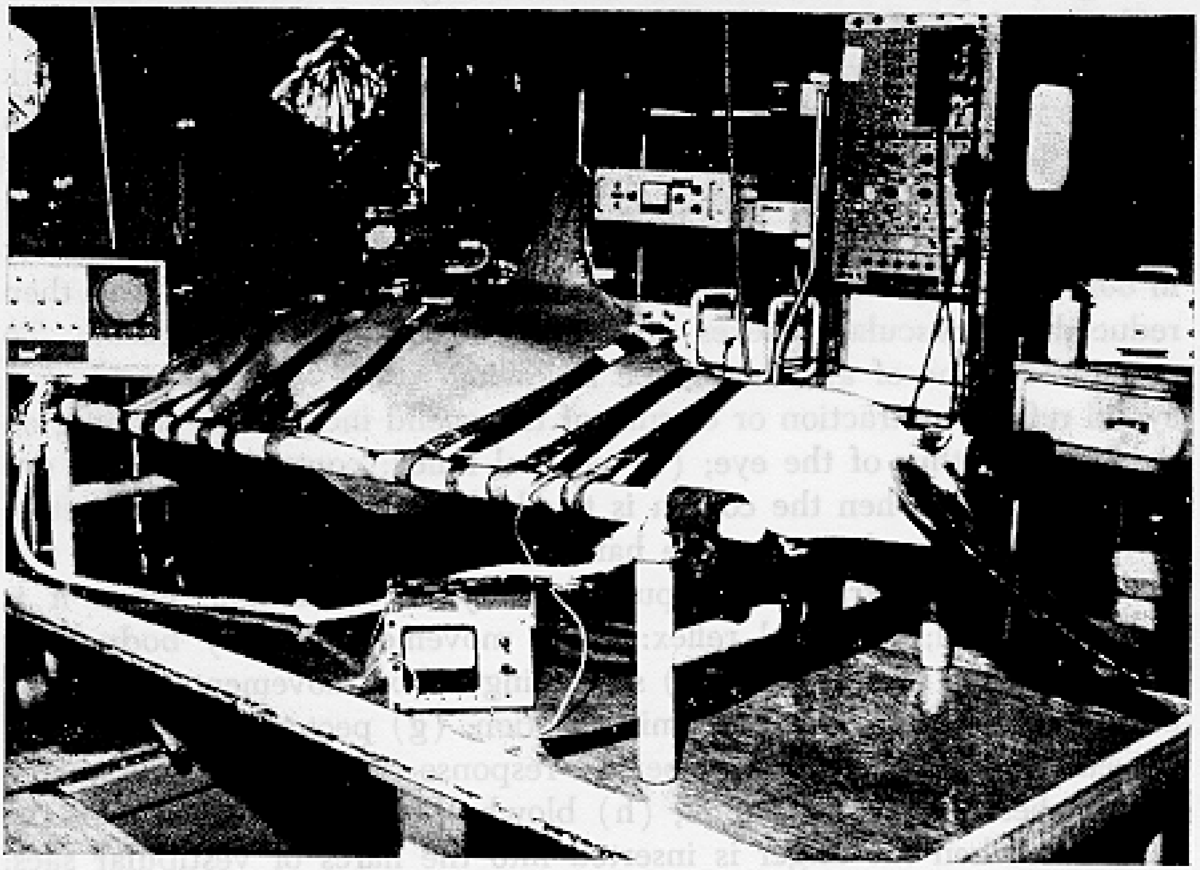

FIG. 18. Porpoise on stretcher in the operating room. Physiological monitoring equipment is in the background. The Bird respirator is in the center just to the right of the porpoise's head.

(Beckman D2), and end tidal pCO_2 concentration of each breath is measured by a Godard capnograph. The electrocardiogram is recorded on a Sanborn 350 recorder, and auditory and visual signals are presented continuously on an electrocardioscope (Electrodyne PMS-5). A urethral catheter is inserted into the urinary bladder, and the urinary output is monitored as an indirect measure of kidney perfusion. During our previous work the urinary output has ranged from 0.7 to 1.5 ml per minute. These values are within normal limits established for unanesthetized animals. The heart rates of the anesthetized animals are very regular, usually ranging from 100 to 120 beats per minute. The normal cyclic variation of heart rate is not present during anesthesia.

A venipuncture is made in the central veins of the flukes, and thiopental sodium (10 mg/kg) is administered to facilitate endotracheal intubation. A 24–30 mm Rusch equine endotracheal catheter with inflatable cuff is employed. While an attendant holds the relaxed jaws open with soft towels, the glottis is pulled anteroventrally from its intranarial position and two fingers are placed inside. The catheter is then passed through the palm of the hand and into the glottis. The cuff is inflated with 50–150 ml of air, and positive-pressure resuscitation is started.

For control of respiration and anesthetic administration, the Bird Mark 9 respirator with apneustic plateau unit is used as a controlled open system in conjunction with the Fluotec Mark 2 vaporizer. A large water vaporizer is also placed in the line to provide for adequate humidification of the respiratory gas mixture. Two percent halothane (in air or in 60% air and 40% oxygen) is administered for a few minutes and then reduced as muscular reflexes and physiological measures indicate. To assess the plane of anesthesia, the following reflexes are observed: (a) eyelid reflex: contraction or closure of the eyelid induced by tapping on the inner canthus of the eye; (b) corneal reflex: contraction of the eye muscles or lids when the cornea is touched; (c) gag reflex: contraction of the throat muscles when the hand is inserted into the pharynx; (d) tongue reflex: contraction or pulling away of the tongue when it is pulled forward; (e) anal reflex: reflex movements of any body parts when the anus is distended; (f) swimming reflex: movements of the tail flukes up and down in a swimming motion; (g) pectoral scratch reflex: movements of the pectoral flippers in response to a pin prick or scratch of the chest or axillary region; (h) blowhole reflex: movements of the blowhole when the finger is inserted into the nares or vestibular sacs; (i) vaginal or prepuce reflex: movements of the vagina or penis, or other body parts when the prepuce or vagina are distended by insertion of the finger or other instrument.

Swimming movements of the free tail flukes have been the most reliable indication of depth of anesthesia. When these movements disappear the subject is sufficiently anesthetized for surgery to begin. During induction the swimming movements disappear just after the loss of strong corneal and eyelid reflexes. The proper plane of anesthesia is maintained with the lowest concentration of halothane necessary to inhibit movement of the tail flukes. The lid and corneal reflexes are the next most dependable criteria for assessing plane of anesthesia.

Anesthesia can be maintained with 0.5–1.0% halothane. Occasionally it may be necessary to increase the concentration to 1.5% for a minute or two to maintain the proper depth of anesthesia. When the halothane is terminated, 60% ambient air and 40% oxygen is administered for the recovery period. Depending on the duration of anesthesia, the animal will usually be awake in 10–15 minutes, and all reflexes except blowhole reflex will be present. The blowhole reflex returns 15–45 minutes later, and at this time extubation can be safely performed. If the animal does not breathe normally within 3 or 4 minutes after the endotracheal tube is removed, it should be reintubated and positive pressure breathing resumed for a few more minutes. After the porpoise is breathing voluntarily it should be placed back into the water, where the buoyancy of its own body will minimize resistance to breathing.

G. Surgery

Until recently, surgical procedures in porpoises were limited to biopsies and other such procedures that could be performed with local infiltration. Techniques for general anesthesia have now made surgery possible in cetaceans. A number of experimental procedures and a few clinical surgeries have been carried out.

Since we have been interested in the reproductive cycles in marine mammals and the possible behavioral changes produced by removal of the gonads, two ovariohysterectomies were performed on adult female *Tursiops*, and an orchidectomy was performed on an adult male. Over a year after the surgery the spayed females are in excellent health and are involved in behavioral and physiological studies. The male, however, died 6 days after the surgery. A postmortem examination indicated that death was due to an infection that was aggravated by the surgery. This animal had been in captivity only 1 week when the operation was performed and thus was a very poor surgical risk.

We have also used the halothane anesthesia technique, described earlier, for a laparotomy, the removal of a cyst, and the repair of a corneal ulcer. Each of these animals recovered completely. We have developed a surgical approach to the porpoise ear, and have used this procedure for making recordings of cochlear potentials and studying the auditory physiology of these animals.

Despite the fact that the animals must go back into the water and swim almost immediately after the operation, healing of the surgical incision has been relatively rapid. Clean sea water is apparently a very good medium for wound healing. A high percentage of *Tursiops* carry scars that are results of apparently severe wounds acquired in their natural habitat.

Because the skin and blubber are contiguous and together form a tough, fibrous integument, heavy suture needles such as those used in bovine surgery are employed. After abdominal surgery the thick abdominal musculature must be sutured well since the animal must use these muscles for swimming very soon after the operation. For this same reason, care should be taken to stay in the midline when making initial abdominal surgical incisions.

I have administered only penicillin and injectable vitamin B_{12} as post-surgical medication. In the limited experience obtained to date, this treatment has been adequate except for the orchidectomy case where a severe enteritis, compounded by the stress of initial introduction into captivity, and the operation, resulted in a fatality.

VI. Behavior and Husbandry

A. Feeding and Nutrition

In the wild, *Tursiops* apparently feeds on a wide variety of fishes, and some squid may be consumed also. In captivity, however, it is rare that these animals will take squid. Some other species of small toothed whales feed predominantly on squid, both in the wild and in captivity.

Food fish for captive porpoises is normally stored in a frozen state and thawed before feeding. The fish is usually acquired from sea food dealers and is of a quality judged fit for human consumption. Wood *et al.* (1966) reported that *Tursiops* at Marineland of Florida were maintained in good health on butterfish (*Poronotus*) and blue runner (*Carnax crysos*) without the addition of food supplements. Thus, it appears that for conditions existing in that oceanarium at least, these two species of fish provided all the necessary dietary requirements to maintain the animals in good health. Herbivorous fishes apparently do not store sufficient vitamins and thus porpoises subsisted on one of these fishes (mullet) developed avitaminosis (Wood *et al.*, 1966).

Porpoises (*Tursiops truncatus* and *Lagenorhynchus obliquidens*) fed only frozen mackerel (*Pneumatophorus diego*) developed lesions in the buccal mucosa that resembled clinical scurvy. High levels of ascorbic acid administered to these animals were followed by a regression in the lesions (R. M. Miller and Ridgway, 1963). This group of porpoises were maintained in tanks where the water temperature varied from 50°F to 70°F. It is possible that porpoises in tropical waters might not have vitamin C requirements as high as those maintained in colder waters. To my knowledge, however, no comprehensive work has yet been done to establish the requirements of any of the vitamins or minerals in porpoises.

It appears that some fish may be nutritionally adequate while others apparently are not. Factors involved in handling, processing, and storage of the fish may affect its nutritional quality, and thus there may be variation in food value between different lots of fish of the same species. Therefore, I recommend the addition of vitamin-mineral supplements to the diet (Ridgway, 1965). This can be done by placing vitamin capsules in one of the food fish of each animal. It also appears to be a good practice to vary the diet. At the Navy Marine Bioscience Facility we feed *Tursiops* on three different kinds of fish, Pacific mackerel (*Pneumatophorus diego*), jack mackerel (*Trachurus symmetricus*), and two or three different species of smelt. The varied diet is considered desirable not only from a nutritional standpoint, but because an animal sustained on one type of fish may develop an exclusive taste for that fish and refuse other types. Thus, difficulty may arise if that particular type of fish happens to come into short supply.

B. Newly Captured Animals

As with most wild animals brought into captivity, chances of mortality are far greater during the initial adaptation to the captive environment than at any other time. *Tursiops* which survive the initial 3 months in captivity are likely to adapt well and live for many years if given proper treatment. Animals under 2 years of age or less than 6½ feet in length are not nearly as likely to survive and adapt readily to captivity as are larger animals. Bottlenose porpoises, however, are hardier and adapt much more readily to captivity than any other species of small cetaceans with which I am familiar. This might be explained in part by the fact that this species frequents bays and estuaries and even on occasion swims into freshwater rivers where it may come in contact with many of the microorganisms of the terrestrial environment. Pelagic cetaceans which remain farther at sea would not be nearly as likely to come in contact with terrestrial animal pathogens, for example. Physiological differences are, no doubt, an important factor as well.

Whereas the more pelagic cetaceans are captured in deep water with "hoop nets" or "tail grabbers," *Tursiops* is usually captured in shallow water by encircling a group of animals with a fishing net. Generally the entrapped porpoises become entangled in the net and are removed individually into a small boat and then transported to a larger craft. Also beach sets are used sometimes, in this case the entrapped porpoises are drawn right up to the shore. The newly caught porpoise is laid on a mattress or suspended in a hammock-like sling, covered with a wet sheet and kept moist. Minor wounds are often incurred, for example, lacerations induced by the capture net line and other handling procedures. Thus, the administration of an antibiotic such as penicillin just after capture is desirable. Administration of vitamin B_{12} and B complex may also be beneficial.

Occasionally a new animal will have some trouble orienting itself and swimming when placed back into the water. This is more likely if the newly captured porpoise spends a long time out of water during transport to holding pens. Sometimes human assistance is needed to keep the porpoise from running into the walls of the tank and to start it swimming on its own. Since they are air breathers, porpoises need not be "walked" as sharks sometimes are, but simply given strong pushes and made to swim on their own. Attendants should position themselves around the edge of the tank, and if it appears that the animal is going to strike the wall, it should be turned and then held with its blowhole out of water until it takes one breath, then it should be pushed across the pool rather than being walked or held in the water. Since porpoises have been known to assist each other, the presence of an already adapted animal in the pool might be of assistance to the new animal. It may later be necessary to separate the newcomers if the already adapted animal(s) interfere with attempts to feed.

One of the first problems encountered in the animal's adaptation to its new environment is to get it to feed. This is done by throwing dead fish into the water in front of the animal's rostrum. Some animals will eat almost immediately after being brought into captivity, but it is more common to have the porpoise go 2–5 days before it commences to feed on dead fish. Usually the porpoise will evidence interest in feeding by nudging the fish with its rostrum. Then it will take one in its mouth, shake it a little, and throw it out. Finally, it will take a fish and in the customary manner swallow the whole fish head first.

Some individuals will refuse food for a week or more. Sometimes feeding can be started by introducing live fish into the pool. When the animal starts to feed on live fish, dead food fish is thrown in and the porpoise may start to take these in as well. Rarely an animal will refuse food for such a long period that it is in danger of starvation. In this case, the animal can be fed via stomach tube. One part fish, one part Ringer's solution, vitamin-mineral capsules, and an essential fatty acid supplement may be mixed in a blender and administered via stomach tube in these cases.

C. Captive Environment

Probably the most important single factor in maintaining healthy porpoises is the water supply. The animals should be kept in clean water free of contamination by pathogenic microorganisms and toxic agents.

There are several different approaches for providing water supplies for maintenance of marine mammals. Sea side oceanaria and laboratories use water pumped directly from the ocean or from seawater wells drilled near the shore. At inland locations freshwater is employed. Enough salt (NaCl) must be added to make a solution of 10 parts per thousand, or 1% sodium chloride. This level seems to be about the minimum salt concentration in which *Tursiops* can be maintained over a long period of time. Seawater generally contains 27–35 parts per thousand of sodium chloride.

Tanks or pools for holding animals should be designed so that water circulates well. This will eliminate stagnant areas that build up algae and bacterial growth, and make possible an adequate water turnover rate. Water should be replaced or recirculated through filters as rapidly as possible. It is desirable to have the environmental water completely recirculated or replaced every 4 hours; every 2 hours is even more desirable. This depends, however, on the volume of the holding pool in proportion to the number of animals being kept there.

The water is generally filtered through conventional sand and gravel filters or diatomaceous earth filters. Filtration requirements for a porpoise pool are usually several times as great as for a swimming pool of the same size. Many costly mistakes have been made in providing for water supplies and filtration systems for facilities where porpoises are to be kept.

The addition of chlorine to the water supply is desirable to combat the growth of various microorganisms. The chlorine level should be kept at between 0.1 and 0.4 ppm. The pH of the water should be between 7.2 and 8.2. Although some species of small toothed whales thrive in the very cold waters, *Tursiops* is primarily a tropical animal. The optimum water temperature for *Tursiops* is probably 70–80°F because this is the approximate range of ocean temperatures in those areas where these porpoises are most commonly found. At the Navy Marine Bioscience Facility water temperature varies from 55°F to about 70°F during the course of a year. The air temperature, however, is usually between 60°F and 70°F. *Tursiops* has done well in this environment. At some locations mortality has been high when water temperature has gone below 50°F and has been accompanied by a low air temperature as well.

D. Transportation

Porpoises have been transported by airplane, by truck, and by boat. They have been successfully shipped from the United States to Europe on several occasions. Townsend (1918) describes the transport of *Tursiops* from North Carolina to New York in water-filled boxes. Today porpoises are not generally shipped suspended in water because of the great weight involved, and because of the danger of the animal injuring itself by its own swimming movements and of the possibility that the animal may continuously be tossed against the walls of the container because of movements of the transport vehicle.

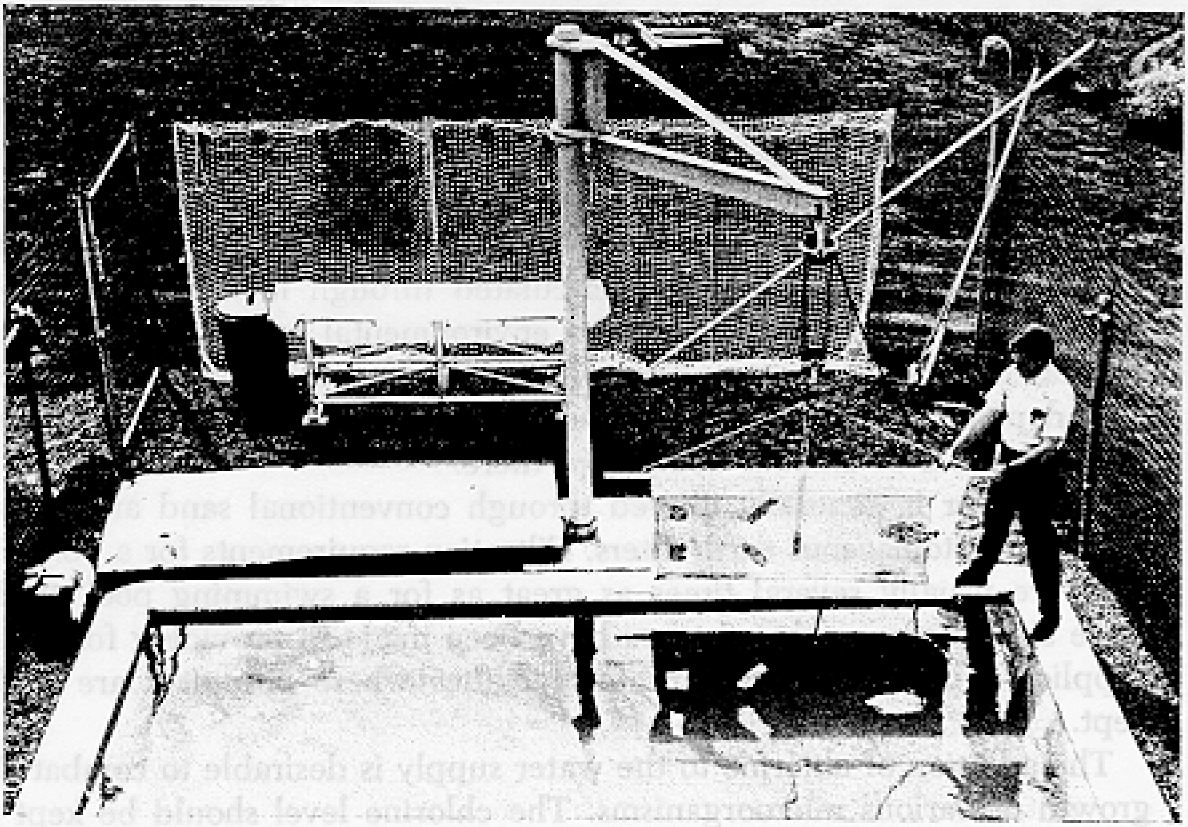

FIG. 19. Transport sling (canvas lined with foam rubber) on lift at Princeton University Porpoise Pool. *Tursiops* can be kept here for studies of auditory physiology. Salt is added to fresh water to make a 1% solution of sodium chloride, which is suitable for maintaining porpoises. Foam rubber pad at left is used as a resting place for porpoises which need to be examined out of the water. The portable surgery cart in the background is equipped with a bag that will hold water. The animal can be placed on the cart and wheeled inside for surgery, examination, or acoustic recording. (Photographs by John Conover, courtesy of Dr. E. G. Wever and James G. McCormick, Princeton University.)

The most frequently used method of transport is to suspend the porpoise in a hammocklike sling. Slits are placed in the sling to accommodate the flippers and/or the eyes. A hole is also provided in the area of the genital slit to provide for drainage of excrement (Fig. 19). The animal is placed in the sling and the sling is suspended in a box or across supports with a bag underneath to catch the water that is sprayed, sponged, or poured over the animal to keep it moist. The porpoise is usually covered with a wet cotton sheet which holds moisture next to the animal.

This minimizes the amount of water required. The sling may be made from heavy linen, canvas, or canvas lined with foam rubber.

Another method frequently employed is to lay the porpoise on its side on a mattress or thick piece of foam rubber inside a box. Waterproof canvas or plastic is used as a liner for the box to produce a bag that can hold water to keep the animal moist. With this method also, the animal is covered with a wet cotton sheet and kept moist. The porpoise should be turned from one side to the other approximately every 2 hours to prevent pulmonary and circulatory congestion and to keep the underside from overheating. No more than 2 or 3 inches of water should be placed in the box, especially if aircraft is to be used. During a nose down attitude of the aircraft, such as on a landing approach, all the water will go toward the front of the box thus covering the blowhole and possibly drowning the animal. It is a good idea to cover the porpoise's eyes with petroleum jelly (without added chemicals) or heavy petrolatum during transport. This provides for retention of the viscous tears around the eye for lubrication and protects the eye from injury due to dust, sand, or other foreign material.

VII. Disease Problems and Therapeutics

The incidence of specific diseases in wild populations of *Tursiops* is not known. Cockrill (1960) reported on a veterinary study of whales caught by whaling ships. According to Cockrill there was a very low incidence of pathology among the whales captured. Nakajima *et al.* (1965) reported 80% mortality of captive porpoises at an oceanarium in Japan over a 7-year period, and this would appear to be only slightly above average for oceanariums and research laboratories throughout the world. At the Navy Marine Bioscience Facility mortality for captive *Tursiops* has been 23% over a period of 5 years. Only two deaths of mature *Tursiops* occurred. Increased collection and dissemination of information about health problems of captive porpoises will likely make possible a reduction in the mortality rate.

Little is known about the virus diseases of marine mammals. A case of clinical jaundice has been reported by Medway *et al.* (1966); however, the etiology has not been established. Virus hepatitis has been suspected, but to my knowledge no case has been confirmed. A confirmed case of diabetes was encountered by Kenney (1965).

A. Respiratory Infections

Pneumonias have probably been the most prominent cause of mortality in captive porpoises. I have encountered pulmonary infections associated with *Diplococcus pneumoniae* staphylococci, and hemolytic streptococci. Often the foci of infection will localize in large lung abscesses. Pulmonary infections are often accompanied by a foul, rancid-smelling breath, and coughing may be noticed. The rectal temperature may rise to 102°F or so, and the white blood cell count is usually increased. The animal may or may not go off its feed.

Cultures can be taken from the blowhole during a breath for antibiotic sensitivity tests. Appropriate antibiotics and fluids, both intravenous and oral, have usually been effective in the treatment of respiratory conditions. Porpoises with pulmonary infections should ke kept out of the water for only minimal periods of time for treatment. Because porpoises swim with only a slight negative buoyancy there is relatively little resistance to breathing while they are in the water. When out of the water the animal must lift much of its own weight to breathe.

B. Erysipelas

The pathology of *Erysipelothix insidiosa* infection (erysipelas in animals, erysipeloid in man) in porpoises has been described by Seibold and Neal (1956), C. F. Simpson *et al.* (1958), and Geraci and Gerstmann (1966). This disease has been one of the most frequent causes of death in captive porpoises. Whether or not the disease occurs in the wild populations is not known. Although food fish has been suspected as the primary route of transmission of the organism, there is little evidence to support this contention. For the present at least, other routes of transmission must be considered along with the fish. It is worthwhile to note that a number of cases of erysipeloid have occurred among persons who performed dissections or postmortem examinations on porpoises or whales.

As in swine, there appear to be different phases of the disease in porpoises. There is an acute phase, or septicemic phase, and a skin phase. In the acute disease the animals will usually go off feed for 1–3 days before death. In one case observed, the animal went off feed on one day and died on the next. Another animal died on the third day after appetite loss. Signs noted were inappetence, lethargy, slow swimming near the surface in stereotyped patterns near the center of the tank, and in the later stages light, rapid respiration (six to eight per minute). Venous blood appeared very dark when drawn into a syringe, indicating a septicemia. Two suspected and three confirmed (by culture of the organism) cases, treated early with large doses of injectable penicillin (two to three million units), Strekacin (Squibb), and fluids via stomach tube, recovered in 3–5 days and no perceptible skin lesions developed.

The skin phase is more prolonged and is characterized by the appearance of large (5–10 cm), usually square or diamond shaped, but sometimes rounded, raised plaques on the surface of the skin. In some cases the plaques occurred with no other signs manifested. In all cases that I am directly familiar with, save one, the disease has been successfully treated after formation of plaques, and on treatment the plaques have regressed. Geraci and Gerstmann (1966) reported three cases that were apparently of the skin type and one of the acute type in which all died. The skin lesions in these cases were not as well defined as those reported by C. F. Simpson *et al.* (1958).

Geraci and Gerstmann (1966) have recommended immunization of animals with commercial bacterin at 6-month intervals. We at the Navy Marine Bioscience Facility have been employing a modified live erysipelas vaccine (2 ml of Norden, Eva) at 6-month intervals, and we have not seen a case of the disease since we started this program almost two years ago. Whether a bacterin or modified vaccine is used, the importance of vaccination of all newly acquired porpoises must be emphasized, both from the standpoint of animal and human health.

C. Gastric Ulcers

Gastric ulcers in marine mammals have been reported by several authors including Schroeder and Wedgeforth (1935), Ridgway and Johnston (1965), and Geraci and Gertsmann (1966). Parasites, dietary histamine, foreign bodies, and the stress of adapting to captivity have been prominent among the causative factors mentioned.

D. Urinary Tract Infections

Urinary tract infections have been observed occasionally. Nitrofuranton (Eaton Laboratories) has been very effective in the treatment of these conditions. I have not employed sulfa drugs in porpoises for fear of possible renal problems.

E. Gastrointestinal Foreign Bodies

Foreign bodies accidentally or purposefully ingested have been among the most serious health problems in captive cetaceans. Several observers have reported cases of ingestion of foreign bodies by porpoises (Brown *et al.*, 1960; Ridgway, 1965; Ameniya, 1962; Nakajima *et al.*, 1965). These small whales have swallowed items such as flash bulbs, coca cola bottles, cups, plastic toys, coins, net floats, plastic bags, various kinds of rubber balls, tin cans, and assorted other paraphernalia.

Just why porpoises tend to swallow items such as these is not known, but there are several possible contributing factors. It is not uncommon to find sand and small stones in the forestomach of wild porpoises. Thus, even some wild animals have the habit of ingesting foreign objects. It has been proposed that stones may be swallowed to aid in the mastication of food since the food is swallowed whole (Slijper, 1958). If this is the case, however, many of them seem to get along perfectly well without the stones. Another possible consideration might be the fact that captive porpoises are conditioned to eat dead fish thrown to them by people and thereafter possibly consider anything thrown into the water as edible. This, however, does not explain why wild animals swallow stones or why porpoises have pulled pieces of plastic sheeting from items near their tank and swallowed them. Often the items which the animals swallow are items that they use as playthings or toys. Thus, performing porpoises in oceanariums have often swallowed balls which they enjoyed throwing and catching. Slijper (1958) attributes the phenomenon to a diminished gustatory sense. Still another possible explanation would be a depraved appetite or a gastrointestinal upset that might result from parasites, enteritis of some type, or ulcers. Dogs and other animals often eat grass, which is to them foreign ingesta, when there is some sort of upset in the gastrointestinal tract. Cattle suffering from various vitamin or mineral deficiencies, such as phosphorus deficiencies, have been known to swallow many different types of foreign objects. This might explain why many captive porpoises never seem to swallow foreign objects, while others do; but it does not explain why porpoises which ingest foreign bodies are frequently the better specimens of a captive group and appear to be in excellent health. Nakajima *et al.* (1965) reported that foreign bodies were found in 18 out of 92 dolphins that died at Enoshima Aquarium in Japan between 1958 and 1965. The largest of these foreign bodies was $35 \times 20 \times 20$ cm and weighed 5 kg. These authors attribute the swallowing of foreign bodies to "some morbid condition of the animals on one hand and excitement in training, showing, or playing on the other." Often, but not always, several items are swallowed rather than just one. One case that I encountered had swallowed three nails, a steel wool cleaning pad, and two washers. The washers and steel wool were removed with a magnet placed into the forestomach. The nails passed on through the gastrointestinal tract, causing no apparent problems. Another porpoise swallowed a silicone rubber suction cup which was used as a blindfold for a poolmate porpoise during some sonar discrimination studies. When several attempts to remove the cup—first by mineral oil (1 liter twice daily) and then by apomorphine injections (which appeared to greatly excite the animal, so much so that Nalorphine had to be given to counteract its affect), and finally by employing a gastroscope and pronged grasper—failed, the porpoise was left alone and appeared to suffer no ill effects for the next year. Slightly over a year later this animal became entangled in a net underwater and drowned. Radiographs taken both shortly after the cup was swallowed and 6 months later revealed that the object stayed in the forestomach. Postmortem examination revealed the cup still in the forestomach along with two large plastic bags, a 4×4 inch gauze square, and a considerable amount of marsh grass. Another porpoise at Hawaii's Sea Life Park swallowed a plastic net float 7 cm long by 4 cm in diameter. This porpoise had not quite reached maturity, and the float was removed by reaching in through the esophagus into the forestomach and pulling the float out with the hand. If the animal had been larger the forestomach could not have been reached; if it had been much smaller the esophagus would not have accommodated an arm and hand. With the development of anesthesia techniques and equipment, surgery is now an alternative if other methods fail.

F. Toxic Agents

1. *Chlorine*

Chlorine added to the water supply has been suspected in cases of corneal ulceration and cloudiness. In these cases the concentration of chlorine has to my knowledge been in excess of 0.4 ppm. I know of no health problems resulting from chlorinated water supplies that have been maintained at levels less than 0.4 ppm. Some problems blamed on chlorine may have resulted from high or low pH.

2. *Histamine*

Certain fishes (Pacific mackerel, *Pneumatophorus diego,* is one) produce great amounts of histamine as they decompose. When the frozen fish is thawed, the histamine level may start to build up. If the fish is kept for a few hours at room temperature or above, considerable amounts of histamine may be produced. Gastric ulceration, apparently caused by dietary histamine, has been described by Geraci and Gertsmann (1966). Acute pulmonary edema might also be caused by exceedingly high levels of histamine in dietary fish.

3. *Copper*

Copper sulfate is another compound that is frequently used for control of algae in water supplies. Prolonged exposure to high levels of copper in the water supply may produce chronic copper poisoning in porpoises. However, this has not been conclusively demonstrated, and maximum levels of long-term tolerance are not known.

G. Skin Conditions

Parasites, metabolic disorders, fungi, sunburn, bacteria, nonspecific purities, bites from pool mates, and other traumatic injuries have caused frequent skin problems in captive porpoises. A clean water supply seems to be the best preventative measure for most of these conditions. A bacterium, *Pseudomonas aeruginosa,* has been frequently cultured from skin lesions in these animals. Since this organism is commonly found in surface waters, it is likely that *Pseudomonas* occurs as a secondary invader more often than as a primary cause.

Animals confined to a small tank or sick animals will sometimes rest for long periods of time on the surface with the blowhole and dorsum of the head out of water. Often these porpoises will sunburn or air burn over that portion of the skin that is exposed to the air. Zinc oxide ointment can be applied to the whole area once each day as a protective measure.

Treatment of other skin lesions consists of removing necrotic tissue, cleaning the lesion thoroughly, and applying topical medication while the animal is out of the water. Before placing the animal back into the water a dye such as pyoktanol or gentian violet may be applied to the affected area since these dyes do not readily wash off. Appropriate systemic therapy must also be employed.

Parasites

A number of investigators have called attention to the large number of parasites found in marine mammals (Delamurye, 1955; Margolis, 1954; Ridgway, 1965; Brown *et al.*, 1960). *Tursiops*, however, appears to have fewer parasite problems than most of the other species. I have encountered slight infestations of a barnacle (*Cirripedia*) which attaches itself to the trailing edges of the flukes or dorsal fin. In no case did the damage appear very serious or widespread, and the barnacles have been seen only on wild porpoises. Apparent copepod infestations have caused severe lesions in the skin and subcutis of a few captive porpoises. A tapeworm, *Diphyllobothrium* sp. and a trematode, *Braunina cordiformis,* have been the most prominent internal parasites that I have encountered in *Tursiops*. *Braunina* are usually found in the main stomach and connecting stomach. Large hard nodules of connective tissue are often found surrounding these parasites. The pathogenesis of *Braunina* in porpoises has been described in Schryver *et al.* (1967).

For control of gastrointestina parasites we have employed Diphentane 70 (Teniatol, Pitman-Moore Co., Indianapolis, Indiana), Thibenzole, Merck and Co., Inc., Rahway, New Jersey), and piperazine phosphate (Candizine, Norden Laboratories, Lincoln, Nebraska). Dosage rate has generally been that recommended for cattle. Piperazine phosphate and thiabendazole are administered routinely every 6 months and diphentane 70 is given only when tapeworms are diagnosed.

H. Drugs and Therapeutic Considerations

I have given most of the common antibiotics, both in injectable and oral forms. There has been some indication that certain porpoises do not tolerate injectable neomycin well. I have not encountered undesirable reactions from oral neomycin or any other antibiotic mixture. Tetracycline, penicillin, streptomycin, colymycin, kanamycin, and chloromycin have been employed most frequently. Steroids such as dexamethasone and flumethasone have been used therapeutically in a number of cases. Injectable vitamin preparations are also frequently used. Dosage rates are figured on a weight basis, using human or bovine recommended dosages depending upon the drug to be employed.

Because of the apparently complicated central nervous system control of respiration, drugs that produce even slight central nervous system depression should be avoided if possible. If light tranquilization is required, small dosages (about one-fourth recommended dosage) of trifluoromeprazine (Nortran, Norden Laboratories), Perphenazine (Trilafon, Schering Corporation), or hydroxyzine (Atarax, Pfizer Laboratories) may be given. McBride and Kritzler (1951) reported that peraldehyde was given in fish to calm excited male porpoises while a female in the same tank was giving birth.

Morphine and apomorphine usually produce excitement when given by injection to porpoises. To my knowledge vomiting has never been produced by apomorphine administration. It is not clear whether the excitatory effect of these drugs is a behavioral sequela to the respiratory depression produced or an actual condition of central nervous system excitement such as is seen in cats. None of the porpoises to which I have given morphine or apomorphine have exhibited the high degree of excitement seen in cats. The reactions have varied from no noticeable change in behavior to marked excitement exhibited by continuous, rapid swimming around the tank. It seems clear that thorough pharmacodynamic studies must be done before any sedatives, hypnotics, tranquilizers, and parasympathomimetic drugs such as atropine can be safely employed in porpoises.

VIII. Clinical Observation of Behavior

A. Reproductive Behavior

McBride and Kritzler (1951) and Tavolga and Essapian (1957) have made observations on pregnancy, parturition, and postnatal behavior in *Tursiops*. Slijper (1966) has described the reproductive system in cetaceans in general, while Wislocki and Enders (1941) have described the placentation of *Tursiops*.

The gestation period is 11 or 12 months. The estrous cycle has not yet been described. The placenta is classified as diffuse epitheliochorial. Pregnancies usually occur in the left horn of the uterus, with a corpus luteum developing on the left ovary. According to McBride and Kritzler (1951), the behavior of the pregnant female cannot be differentiated from that of other individuals until sometime in the second half of the pregnancy. As term approaches the pregnant animal will withdraw from close association with others and show somewhat less interest in play. During the last half of pregnancy the abdomen becomes greatly distended. This is most easily detected by observing the lateral profile where the ventral abdomen passes into the inguinal region and caudal peduncle. The vulva also becomes puffed and wrinkled as term approaches. Animals which have had past pregnancies will often maintain these wrinkles above the vulva.

Normally the fetus is passed tail first in a breech presentation. The periods of delivery of live young observed by McBride and Kritzler (1951) were generally short (20 minutes to 1 hour) but one successful birth lasted 1 hour and 53 minutes. Stillbirths observed by these authors generally lasted much longer. When the fetus is passed the mother whirls about, breaking the umbilical cord and putting herself in position to help the infant up to breathe, but the newborn usually swims to the surface without assistance. In cases observed, the placenta was not passed for some time (up to 10 hours) after birth.

The mother rolls over on one side and glides along in the water while the young suckles. The infant swims just enough to keep up with the mother. The young porpoise grasps the parent's extended nipple between the palate and its tongue, which is held in a grooved position. The mouth is held slightly open. Each suckling lasts only a few seconds and it appears that milk is forcibly expelled from the mammary sinuses of the mother. Although the young porpoise may take whole fish before a year of age it is not weaned until 12 to 18 months of age.

B. Care-Giving Behavior

Caldwell and Caldwell (1966) have reviewed epimeletic (care-giving) behavior in cetaceans. The most common form of this behavior seen in captivity is supporting behavior. There are numerous reports of this behavior in the literature. It is characterized by one or more animals supporting an injured individual animal at the surface. This behavior has most frequently been seen when infant porpoises have been involved. Female porpoises have been observed to support their stillborn young at the surface for considerable periods of time.

C. Other Behavior of Possible Clinical Significance

1. *Lob Tailing*

This behavior is characterized by the animal raising its flukes out of the water and bringing them down on the surface with a whacking motion. This action seems to be in the form of a warning and to me seems to be analogous to the pawing of the ground by a bull. The animal may do this when it is irritated for any reason. It may also be seen as a bluffing gesture during play.

2. *Blowing Bubbles*

Sometimes porpoises will release large quantities of air from the blowhole while stationed 2 or 3 feet under the water. This creates a large bubble which wells up to the surface. In our animals, this is most frequently seen at feeding time and is probably a begging gesture.

3. *Jaw Snapping*

This is usually in the form of a warning and indicates that the animal is angry. The jaws are opened and snapped together hard. This may be accompanied by rigid jerking up and down movements of the head. In those rare cases where people have been bitten by porpoises the bite has usually been preceded by jaw snapping behavior.

4. *Aroused Surfacing*

This behavior is characterized by the animal swimming around the tank with the upper portion of the head and eyes out of the water. The snout may be slightly above the surface, with the rest of the head parallel to the surface. This may be done to allow the animal to get a better view of people and activities around the tank.

5. *Snorting*

This is another behavior that may indicate displeasure. It is characterized by the animal expelling air in such a way as to create a snorting sound. It may be seen in conjunction with aroused surfacing or lob tailing. Snorting must be differentiated from coughing, which may occur during respiratory conditions.

6. *Behavior of Sick Animals*

Loss of appetite is the behavior most generally considered to judge whether or not a porpoise is feeling well. Failure of the animal to feed is not always a good indication of illness. Sometimes these animals will go off feed for a day or two for no apparent reason. When porpoises at our Facility refuse their food, they are taken out of the water and examined. The examination includes collection of blood and urine specimens for hematology, blood chemistry, and urinalysis.

Porpoises that are not feeling well may exhibit lob tailing, snorting, or bubble-blowing behavior. These behaviors are not generally observed in porpoises that are very ill, however. Porpoises that are extremely ill will usually swim in stereotyped circular patterns. They usually do not change the direction of their swimming often and do not seem to pay attention to the activities of poolmates or people around the tank.

IX. Scope and Limitations of *Tursiops* in Biomedical Experimentation

As man becomes more interested in the sea, there will no doubt be greater concern about marine life. Prolonged exposure to the deep ocean environment will likely necessitate increased knowledge in several areas of medical science. Some of the physiological adaptations of porpoises to the ocean environment have already been discussed. Increased knowledge of physiological functions of marine mammals may yield information beneficial to divers and aquanauts of the future.

A. Bionics

The science called bionics is the study of specialized animal systems that might possibly be converted to manmade analogs. Scientists concerned with bionics have been especially interested in porpoises for several reasons. These animals have sensitive broadband hearing. They can apparently hear directionally underwater, a capability which man does not seem to have. Porpoises also have an excellent sonar or echolocation system which allows them to find food, avoid objects, and otherwise gain necessary information about their environment by using sound.

Because *Tursiops* has a very large, well-developed brain, continued interest in the species will be shown by anatomists, neurophysiologists, and those concerned with neural control systems, animal communication systems, and the like.

B. Porpoise Sonar

Echolocation is apparently one of the principal means by which porpoises gain information about their environment. Sound in the form of brief trains of broadband clicks is projected from the animal's larynx or nasal air passages, and return signals are probably processed in the cochlea and the brain to give the porpoise an acoustic picture of that portion of the environment being examined. While echolocating, the animal usually moves its head from side to side in a circular motion as it swims.

The underwater sounds produced by captive *Tursiops* have been described by Wood (1953). Several investigators have reported experimental evidence of the echolocation capability of *Tursiops* (W. N. Kellogg, 1960; Norris *et al.*, 1961; Evans and Powell, 1967; Turner and Norris, 1966; Schevill and Lawrence, 1956). Complicated neural, auditory, and sound production mechanisms as well as physical characteristics of various tissues must be defined before echolocation in porpoises can be completely understood.

C. Limitations

It appears at present that future use of *Tursiops truncatus* as a research animal will no doubt be limited. Several factors contribute to this situation:

1. Initial acquisition cost is relatively high (three hundred to one thousand dollars per animal) depending upon sex, age, condition, and degree of adaptation to captivity desired.

2. Extensive facilities are required. These include a good water supply, tanks, filters, food storage, and equipment for handling the animals.

3. The cost of maintenance of both facilities and animals is also high in terms of manpower and dollars. An adult *Tursiops* requires between $60 and $100 of food each month.

However, there appears to be a great deal to learn from these animals, and no doubt a high level of interest in them will continue.

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References

Amemiya, I. (1962). *Intern. Zoo Yearbook* 4, 34.

Breathnach, A. S. (1960). *Biol. Rev.* 35, 187–230.

Brown, D. H., McIntyre, R. W., Delli Quadri, C. A., and Schroeder, R. J. (1960). *J. Am. Vet. Med. Assoc.* 137, 534–538.

Burne, R. H. (1952). "Handbook of Cetacean Dissections." British Museum (Natural History), London.

Caldwell, M. C., and Caldwell, D. K. (1966). *In* "Whales, Dolphins and Porpoises" (K. S. Norris, ed.), pp. 755–789. Univ. of California Press, Berkeley, California.

Cockrill, W. R. (1960). *Brit. Vet. J.* 116, 1–28.

Coulombe, H. N., Ridgway, S. H., and Evans, W. E. (1965). *Science* 149, 86–88.

Delamurye, C. L. (1955). "Helminth Fauna of Marine Mammalia in Light of Their Ecology and Phylogeny." Acad. Sci. U.S.S.R., Moscow.

Duffield, D. A., Ridgway, S. H., and Sparkes, R. S. (1967). *Nature* 213, 189.

Eichelberger, L., Geiling, E. M. K., and Vos, B. J. (1940). *J. Biol. Chem.* 133, 661.

Elsner, R., Kenney, D. W., and Burgess, K. (1966). *Nature* 212, 407–408.

Evans, W. E., and Powell, B. A. (1967). *In* "Animal Sonar Systems" (R. G. Busnel, ed.), Vol. 1, pp. 363–383. Lab. Physiol. Acoustique, Jouy-en-Josas, France.

Felts, W. J. L., and Spurrell, F. A. (1965). *Am. J. Anat.* 116, 171–203.

Felts, W. J. L., and Spurrell, F. A. (1966). *Am. J. Anat.* 118, 103–134.

Fetcher, E. S., and Fetcher, G. W. (1942). *J. Cellular Comp. Physiol.* 19, 123–130.

Fiebiger, J. (1916). *Anat. Anz.* 48, 640.

Flanigan, N. J. (1966). *In* "Whales, Dolphins and Porpoises" (K. S. Norris, ed.), p. 130. Univ. of California Press, Berkeley, California.

Gardner, M. (1967). Personal communication.

Geraci, J. R., and Gerstmann, K. E. (1966). *J. Am. Vet. Med. Assoc.* 149, 884–890.

Green, R. F. (1968). *In* "Marine Mammals: Biology, Medicine, and Husbandry" (S. H. Ridgway, ed.). Thomas, Springfield, Illinois (in preparation).

Heezen, B. C. (1958). *Deep-Sea Res.* 4, 665.

Horvath, S. M., Chiodi, H., Ridgway, S. H., and Azar, Sam (1968). *Comp. Biochem. Physiol.* 24, 1027.

Howell, A. B. (1930). "Aquatic Mammals," p. 338. Thomas, Springfield, Illinois.
Huber, E. (1934). *Carnegie Inst. Wash. Publ.* **447**, 105–136.
Irving, L., Scholander, P. F., and Grinnell, S. W. (1941). *J. Comp. Physiol.* **17**, 145–168.
Jablokov, A., and Belkovitsch, V. M. (1962). *Eston. Nature* **142**, 148.
Johnson, C. S. (1966). *Naval Ordinance Test Sta., Tech. Rept.* **4187**.
Kanwisher, J., and Sundnes, G. (1966). *In* "Whales, Dolphins and Porpoises" (K. C. Norris, ed.), p. 210. Univ. of California Press, Berkeley, California.
Kellogg, R. (1931). *Quart. Rev. Biol.* **3**, 29–76 and 174–208.
Kellogg, W. N. (1960). *Psychol. Record* **10**, 25–27.
Kenney, D. W. (1965). Unpublished data, Del Mar, California.
Krogh, A. (1939). "Osmotic Regulation in Aquatic Animals," pp. 162–165. Cambridge Univ. Press, London and New York.
Langworthy, O. R. (1931). *J. Mammal.* **12**, 381–389.
Langworthy, O. R. (1932). *J. Comp. Neurol.* **54**, 437–500.
Lawrence, B., and Schevill, W. E. (1954). *J. Mammal.* **35**, 225–232.
Lawrence, B., and Schevill, W. E. (1956). *Bull. Museum Comp. Zool. Harvard* **114**, 103–152.
Lawrence, B., and Schevill, W. E. (1965). *Bull. Museum Comp. Zool. Harvard* **133**, 6–58.
Laws, R. M. (1953). *Nature* **169**, 972.
Lilly, J. C. (1962). "Man and Dolphin," pp. 46–57. Gollancz, London.
Lilly, J. C. (1964). "Handbook of Physiology—Environment," pp. 741–747.
Lilly, J. C., and Miller, A. M. (1962). *J. Comp. Physiol. Psychol.* **55**, 73–79.
McBride, A. F., and Hebb, D. O. (1948). *J. Comp. Physiol. Psychol.* **41**, 111–123.
McBride, A. F., and Kritzler, H. (1951). *J. Mammal.* **32**, 251–266.
McCormick, J. G. (1967). Master's Thesis, Psychology Library, Princeton University.
McCormick, J. G., Wever, E. G., and Ridgway, S. H. (1968). *Ann. Conf. Am. Psychol. Assoc., San Francisco.* (Twenty-minute movie with abstract in proceedings.)
MácKay, R. S. (1964). *Science* **144**, 864.
Margolis, L. (1954). *J. Fisheries Res. Board Can.* **11**, 267–283.
Medway, W., and Geraci, J. R. (1964). *Am. J. Physiol.* **207**, 1367–1370.
Medway, W., and Geraci, J. R. (1965). *Am. J. Physiol.* **209**, 169–172.
Medway, W., Schryver, H. F., and Bell, B. (1966). *J. Am. Vet. Med. Assoc.* **149**, No. 7, 891–895.
Miller, R. M., and Ridgway, S. H. (1963). *Small Animals Clinician* **3**, 189–193.
Miller, G. S. (1923). *Smithsonian Inst. Misc. Collections* **76**, 1–71.
Nagel, E. L., Morgane, P. J., and McFarland, W. L. (1964). *Science* **146**, 1591.
Nagel, E. L., Morgane, P. J., and McFarland, W. L. (1966). *Vet. Med. Small Animal Clinician* **61**, 233.
Nakajima, M., Sawawia, K., Fujimoto, A., and Tetsunosuke, O. (1965). "Foreign Bodies in the Stomachs of the Captive Dolphins," Vol. 11, p. 27. Enoshima Marineland, Enoshima, Japan.
Nishiwaki, M., and Yagi, T. (1954). *Proc. Japan Acad.* **30**, 399.
Norris, K. S., Prescott, J. H., Asa-Dorian, P. V., and Perkins, P. (1961). *Biol. Bull.* **120**, 163–176.
Odend'hal, S., and Poulter, T. C. (1966). *Science* **153**, 768–769.
Palmer, E., and Weddell, G. (1964). *Proc. Zool. Soc. London* **143**, 553.
Parry, D. A. (1949). *J. Exptl. Biol.* **26**, 24.
Purves, P. E. (1967). *In* "Animal Sonar Systems" (R. Busnel, ed.), Vol. I, p. 197. Lab. Physiol. Acoustique, Jouy-en-Josas, France.

Purves, P. E., and Van Utrecht, W. L. (1963). *(Amsterdam) Beaufortia* 9, 241–256.
Ridgway, S. H. (1965). *J. Am. Vet. Med. Assoc.* 147, 1077–1085.
Ridgway, S. H. (1966). *Proc. 3rd Ann. Conf. Biol. Sonar Diving Mammals, 1966* pp. 151–158. Stanford Research Inst., Menlo Park, California.
Ridgway, S. H., and Green, R. F. (1967). *Norsk Hvalfangst-Tidende* 1, 1–8.
Ridgway, S. H., and Green, R. F. (1968). In preparation.
Ridgway, S. H., and Johnston, D. G. (1965). *Am. J. Vet. Res.* 26, 771–775.
Ridgway, S. H., and Johnston, D. G. (1966). *Science* 151, 456–458.
Ridgway, S. H., and McCormick, J. G. (1967). *Science* 158, 510.
Ridgway, S. H., Flanigan, N. J., and McCormick, J. G. (1966). *Psychon. Sci.* 6, 491.
Ridgway, S. H., Simpson, J. G., and Patton, G. S. (1968). *Proc. 2nd Conf. Diseases Aquatic Mammals, Boca Raton, Florida.* In press.
Schevill, W. E., and Lawrence, B. (1953). *J. Exptl. Zool.* 124, 147–165.
Schevill, W. E., and Lawrence, B. (1956). *Brev. Museum Comp. Zool.* 53, 1–15.
Schevill, W. E., and McBride, A. F. (1956). *Deep-Sea Res.* 3, 153–154.
Scholander, P. F. (1940). *Hvalradets Skrifter Norske Videnkaps-Akad. Olso* 22, 4.
Scholander, P. F., and Schevill, W. E. (1955). *J. Appl. Physiol.* 8, 333–342.
Schroeder, C. R., and Wedgeforth, H. M. (1935). *J. Am. Vet. Med. Assoc.* 87, 333–342.
Schryver, H. F., Medway, W., and Williams, J. F. (1967). *J. Am. Vet. Med. Assoc.* 151, 884–886.
Seibold, H., and Neal, J. E. (1956). *J. Am. Vet. Med. Assoc.* 128, 537–538.
Sergeant, D. E. (1959). *Norweg. Whaling Gaz.* 6, 273.
Simpson, C. F., Wood, F. G., Jr., and Young, F. (1958). *J. Am. Vet. Med. Assoc.* 133, 558–560.
Simpson, J. G., and Gardner, M. (1968). *In* "Marine Mammals: Biology, Medicine, and Husbandry" (S. H. Ridgway, ed.). (in preparation). Thomas, Springfield, Illinois.
Slijper, E. J. (1958). "Whales" (transl. by A. J. Pomerans). Hutchinson, London.
Slijper, E. J. (1966). *In* "Whales, Dolphins and Porpoises" (K. C. Norris, ed.), p. 306. Univ. of California Press, Berkeley, California.
Tavolga, M. C., and Essapian, F. S. (1957). *Zoologica* 42, 11–31.
Tomilin, A. G. (1957). "Animals of the USSR and Adjacent Countries," Acad. Sci. USSR, Moscow. Vol. 9, pp. 190–215.
Townsend, C. H. (1918). *Zoologica* 1, 289–299.
Turner, R. N., and Norris, K. S. (1966). *J. Exptl. Anal. Behavior* 9, 535–544.
Walen, K. H., and Madin, S. H. (1965). *Am. Naturalist* 99, 349.
Wislocki, G. B. (1929). *Am. J. Anat.* 44, 47–77.
Wislocki, G. B., and Enders, J. (1941). *Am. J. Anat.* 68, 97–125.
Wood, F. G., Jr. (1953). *Bull. Marine Sci. Gulf Caribbean* 3, 120–133.
Wood, F. G. Jr., Norris, K. S., Dudok Van Heel, W., and Ray, C. (1966). *In* "Whales, Dolphins and Porpoises" (K. C. Norris, ed.), p. 650. Univ. of California Press, Berkeley, California.